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The Salmon Terminal Fishery: a Practical, Comprehensive Timing Model

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SCHNUTE, J., AND J. SIBERT. 1983. The salmon terminal fishery: a practical, comprehensive timing model. Can. J. Fish. Aquat. Sci. 40: 835–853.

This paper presents a comprehensive model for analysis of data from a salmon terminal fishery. The model includes a new description of salmon run curves, tailored form earlier models of biological growth. It also includes a new equation to describe the process of fishing from a pool of fish that belong to various stages of the salmon run. It allows for variable run timing between fishery and hatchery, and it incorporates test fishery data in a systematic way. A likelihood function is derived that gives an objective criterion for estimating parameters associated with run timing, the fishery, and the test fishery. The model is applied to 4 yr of historical data on the chinook (*Oncorhynchus tshawytscha*) fishery in Barkley Sound and Alberni Inlet, British Columbia, Canada. Run timing proves to be remarkably consistent from year to year. Time spent by the fish in the fishery is ill-determined from the data, but most other important parameters are relatively insensitive to this uncertainty.

SCHNUTE, J., AND J. SIBERT. 1983. The salmon terminal fishery: a practical, comprehensive timing model. Can. J. Fish. Aquat. Sci. 40: 835–853.

On trouvera dans l'article qui suit un modèle complet d'analyse de données relatives à une pêcherie terminale de saumon. Incluse dans ce modèle est une nouvelle description des courbes de remontes des saumons, élaborées à partir de modèles antérieurs de croissance biologique. Il contient aussi une nouvelle équation décrivant le processus de pêche d'un groupe de poissons appartenant à divers stades de remonte. Le modèle tient compte des différences, entre pêche et écloserie, des temps de remonte, et incorpore de façon systématique les données sur des pêches d'essai. On obtient ainsi une fonction de probabilité, qui est un critère objectif d'estimation des paramètres associés à la chronologie des remontes, à la pêcherie et aux pêches d'essai. Nous appliquons le modèle à une série de quatre ans de données sur la pêcherie de saumon chinook (*Oncorhynchus tshawytscha*) de la baie Barley et de l'inlet Alberni, en Colombie-Britannique (Canada). La chronologie des remontes se montre remarquablement uniforme d'une année à l'autre. Le temps que les poissons passent dans la pêcherie est mal défini par les données, mais la plupart des autres paramètres importants sont relativement insensibles à cette incertitude.

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As salmon migrate back to their home stream to spawn, they may be caught in a variety of fisheries along the migration path. The final such fishery, called a terminal fishery, typically occurs in a bay or inlet at the mouth of the home stream. Here, fishermen have a last chance to harvest the run, and fishery managers have a final opportunity to preserve enough of the run for spawning requirements. The consequences of inappropriate management actions in the terminal fishery eventually become painfully evident. On the one hand, if too much fishing is allowed, the resulting low escapement poses a possible threat to the next cohort. On the other hand, if too few fish are harvested, an evident excess of spawners may cause fishermen to cry foul because a valuable opportunity has been lost. Unfortunately for the manager, there usually is a time lag of weeks or months before the spawner count is available. Thus, the information to judge the success or failure of management comes too late to be of use in making decisions but soon enough to arouse an angry public in the event of failure.

Essentially, the manager's problem in this situation is to discover the size of the run as it occurs, so that an appropriate harvest can be allowed. The fishery itself can be used as an indicator of run size, but this is sometimes risky because a small run might be devastated before its small size is detected. Partly for this reason, a test fishery may be conducted to give a preliminary run estimate before opening the commercial fishery. In addition, if the test fishery is maintained for most of the run, it can be used to gain knowledge of run timing. Such knowledge has considerable potential value for future years in cases where timing of the run tends to be consistent from year to year.

In summary, the manager of a salmon terminal fishery is faced with a rather complex set of indicators on which to base the decision to open or close the fishery. The first step in the analysis of these indicators involves a study of their past significance. For example, past test fisheries could be used to discover the relationship between catch per unit effort and population size. Given the historical escapements, it is reasonable to try to reconstruct past runs, that is, to describe completely how many fish were in the fishery each day and to break down the daily population into catch, test catch, and escapement. If historical data are available for several years, such an analysis would reveal much about the consistencies and irregularities of the fishery.

This paper presents a new, comprehensive approach to the analysis described above. It requires detailed data on catch, test catch, and escapement. Typically, escapement data are available in sufficient detail only for hatchery runs of fish. The analysis is based on a model with five main assumptions. (1) Fish arrive in the fishery according to a smooth curve characterized by a single peak and arbitrary skewness and flatness. (2) Fish remain in the fishery for a fixed period of time, which may be days or even weeks. During this period they remain equally vulnerable to capture. (3) Test catch per unit effort is proportional to the current fishery population. (4) For every day on which fish enter the fishery, there is a corresponding day on which they arrive in the hatchery. The time lag between fishery and hatchery need not be constant; for example, fish that arrive early in the fishery may take longer to reach the hatchery than fish that arrive late. (5) The catch and test catch account for all mortality during the time between entry to the fishery and arrival at the hatchery.

Earlier analyses of terminal fishery data, to the extent they exist in management practice, typically deal with only parts of the problem solved here and involve more restrictive assumptions. In contrast with assumption 1, the common assumption is that the run follows a normal (nonskew) curve. Also, in contrast with assumption 2, fish are usually implicitly assumed to remain only briefly in the fishery, so that a day's catch comes from only a day's segment of the run. Finally, it is customary to presume a constant time lag between fishery and hatchery, typically determined by a tagging experiment. The model here admits all these possibilities as special cases: symmetric run curves, brief fishery residence, and constant migration time between fishery and hatchery. However, data presented here give evidence for rejecting all these restrictive assumptions. Incidentally, the analysis here could easily accommodate tagging data if available but does not require it because the relationship between fishery and escapement data can be used to infer the unknown time lag.

The paper concludes with a worked example based on data compiled by Sibert and Schnute (1982) for the chinook salmon run into Alberni Inlet and the Robertson Creek Hatchery on Vancouver Island, British Columbia, Canada. Results from independent analyses for the 4 available yr with test fishery data (1978–81) are presented in detail.

Terminal Fishery Model

Overview

Like most real world situations, the terminal fishery is complex. A serious attempt to model it must mirror that complexity, even if it means using an elaborate notation. As a guide to the reader, Appendix A lists alphabetically all notation in this paper. The sections below describe the model in detail sufficient for a practitioner to implement it as a computer program. The overview here is intended to direct attention to the model's key features.

The model involves five main components. First, there is a (possibly skewed) bell-shaped curve that describes the rate at which salmon enter the fishery. Suitable equations are given in the section on salmon run curves. Second, there is the process by which fish accumulate in a fishery pool and are exposed to capture. This process is rather complex because fish continually enter and leave the pool while residents are caught. Any particular resident becomes more exposed to capture as the number of fish in the pool diminishes. The pool size is thus a function of its history, and this is described mathematically in the section on pool time in the fishery.

The third component, identified in the section on salmon run curves, involves a (possibly variable) time lag between fishery and hatchery. The assumption here is that the time lag is a linear function of time: if it is 60 d at the beginning of the run and 30 d at the end, it will, for example, be 45 d at the midpoint of the run. The fourth component concerns the test fishery. In a section on the composite model, the usual assumption is made that the test catch per unit effort is proportional to the available population.

The fifth and final component deals with variability. Since

the data never fit the model exactly, it is necessary to describe the noise, that is, the statistical process whereby observations depart from predictions. This component of the model is very important because the statistical "likelihood" function (derived in a section so named) provides an objective criterion for estimating the model parameters: the best estimates are those that give the most likely explanation of observed data. A given set of model parameters determines a theoretical run of fish, and the likelihood is calculated from this run. The most difficult computational step involves projecting the escapement back into the fishery and adding the observed catch back into the run in a rather complex way, a process called "back calculation." The section on pool time in the fishery develops notation and concepts necessary for back calculation.

Even though fishery and hatchery activities occur on a daily basis, it turns out that the best analytic framework for this problem includes time as a continuous variable; time t need not be an integer. The model involves, for example, both the cumulative catch $C(t)$ and its derivative, the catch rate $c(t)$. Typically, a cumulative function is represented in uppercase and the corresponding rate in lowercase. The units of C and c are fish and fish per day, respectively; in practical terms, however, $C(t)$ and $c(t)$ can be considered "the total catch up to day t" and "the daily catch on day t", respectively. Strictly speaking, these phrases are incorrect because time t need not be an integer day and $c(t)$ is a rate of catch. The discussion below includes such liberties with the language as an aid to the reader's intuition, since the notation itself implies precise dimensional units.

The model given here ultimately involves eight unknown parameters: three to describe a smooth run curve, two to define the variable time lag between fishery and hatchery, one to specify the time spent in the fishery pool, and two to identify the catchability and an associated error in the test fishery. There are, however, many equivalent ways to specify these eight parameters, and it is not a priori clear which is best for a particular problem. For this reason, transformations among various parameters are derived in the sections following, and as in the example worked here, the practitioner is encouraged to try several possibilities and to determine those that produce the most stable results.

This section can be used as a guide for the first reading of the technical material following. Focus on the features outlined above and give cursory attention to computational details ultimately needed for a precise computer implementation.

Salmon Run Curves

Let $X(t)$ represent the total (cumulative) number of fish that have entered the fishery at time t, where t is measured in days. Then the daily rate at which fish enter the fishery is the derivative $x(t) = dX/dt$. Usually, the graph of $x(t)$ is a bell-shaped curve, such as the normal curve, and $X(t)$ is S shaped (see Walters and Buckingham 1975, p. 113). There are two disadvantages, however, in assuming that $x(t)$ is normal. First, the actual run of fish may be skewed; for example, the first half of the run may come in gradually, while the final half arrives quickly. The symmetric normal distribution does not admit this possibility. Second, if $x(t)$ is normal, then the integral $X(t)$ cannot be represented analytically. Given computers, this is a minor problem, but it is often a nuisance.

The problem of finding a versatile and convenient description of a salmon run can best be solved with reference to the cumulative run $X(t)$, rather than the rate $x(t)$. Suitable S-shaped curves are documented in the context of fish growth, for example, by Schnute (1981). A curve of the Richards type,

$$(1) \quad X(t) = X_\infty [1 - be^{-a(t-\tau^*)}]^{1/b},$$

usually works very well. Curve (1) belongs to a general family of growth curves discussed by Schnute (1981), and it contains the four parameters X_∞, τ^*, a, and b. Here, X_∞ represents the number of fish in the entire run, a number that is known for historical runs from the total catch and escapement. The parameter τ^* is the time when $X(t)$ has an inflection point and $x(t)$ has a peak.

To interpret a and b, let X^* and x^* represent $X(\tau^*)$ and $x(\tau^*)$, respectively, and define the two additional parameters

$$X' = X^*/X_\infty,$$

$$x' = x^*/X_\infty.$$

Then, X^* is the total number of fish that arrive by the peak day τ^*, and X' is the corresponding fraction of the entire run. For instance, if X' equals 0.3, this means that 30% of the run arrives by the peak day. Consequently, the run curve $x(t)$ has a shorter left than right limb, and it is skewed left. Similarly, x^* is the peak number of fish that arrive per day, and x' is the corresponding peak daily fraction. If, for example, x' is 0.06/d, this means that 6% of the entire run arrives on the peak day τ^*. It turns out (Appendix B) that

$$(2) \quad X' = (1 - b)^{1/b}$$

and

$$(3) \quad x' = a(1 - b)^{(1-b)/b}.$$

From equation (2), the parameter b determines X', and, given a value of b, the parameter a then determines x' by equation (3). In fact, equations (2) and (3) show that the parameter pairs (a, b) and (X', x') are equivalent; that is, the same run curve can be described with either pair.

Notice in equation (2) that if $b = -1$, then $X' = 0.5$; in other words, exactly 50% of the total run arrives by the peak day, and the run curve $x(t)$ is symmetric. It turns out that if $b > -1$, then $X' < 0.5$, that is, $x(t)$ is skewed left. Similarly, $b < -1$ implies that $X' > 0.5$ and $x(t)$ is skewed right. Consequently, b can be interpreted as a skewness parameter. The interpretation of a is even simpler by equation (3): a is directly proportional to the peak daily run fraction x'.

In principle, equations (2) and (3) make it possible to recast curve (1) in terms of the parameter set $(X_\infty, \tau^*, X', x')$ rather than (X_∞, τ^*, a, b). Unfortunately, equation (2) cannot be solved analytically for b; however, equation (3) at least allows a to be eliminated in favor of the parameter x'. From equations (1) and (3)

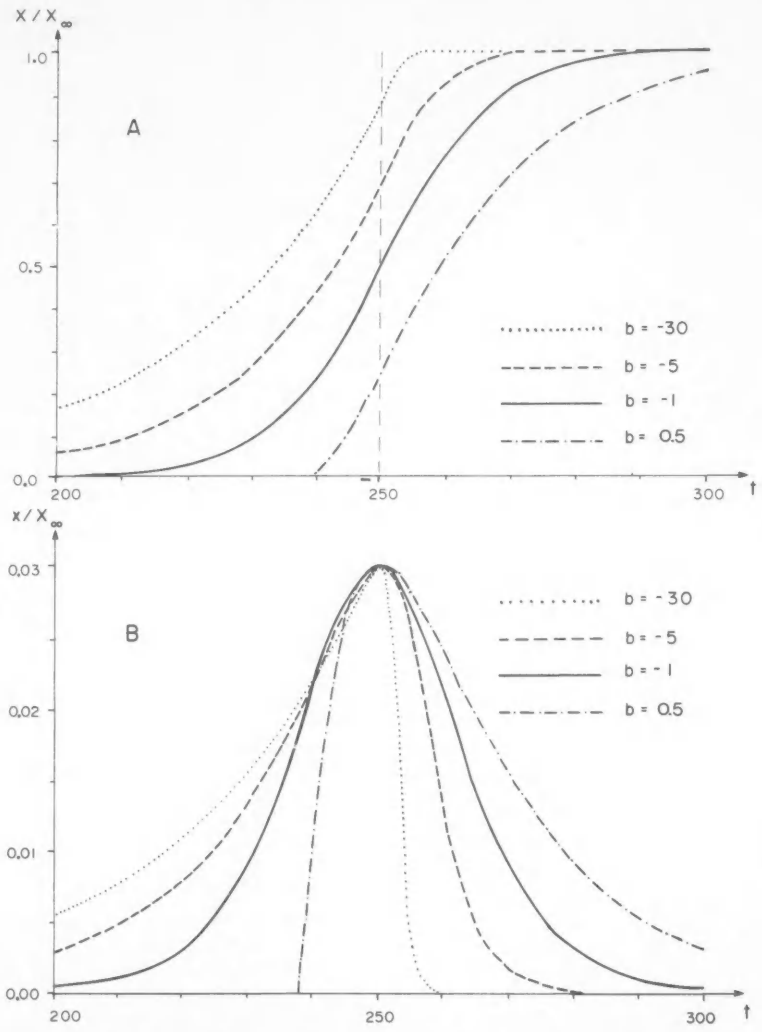


FIG. 1. Cumulative run curves (A) and daily run curves (B) for four values of the skewness parameter b. Values of $X(t)$ and $x(t)$ are shown in relation to the total run X^*. The curves all share the parameter values $\tau^* = 250$ and $x' = 0.03$, which are roughly those of the run into the fishery for the example worked in this paper. In Fig. 1A, the curves all have an inflection point at $t = 250$, and the vertical broken line aids this perception. The curves in Fig. 1B all take a maximum value of 0.03 at $t = 250$.

$$(4) \quad X(t) = X_\infty \{1 - b \exp [-x'(1 - b)^{-(1-b)/b} \times (t - \tau^*)]\}^{1/b}.$$

This version of equation (1), although somewhat complex, involves the three biologically meaningful parameters X_∞, τ^*, and x', as well as the skewness parameter b. Figure 1 shows $X(t)$ and $x(t)$ for various values of b, with the remaining parameters held fixed.

It is possible to solve equation (4) for t with the result

$$(5) \quad t = \tau^* - x'^{-1} (1 - b)^{(1-b)/b} \log \{[1 - (X/X_\infty)^b]/b\}.$$

Notice that equation (5) involves the ratio $X(t)/X_\infty$, that is, the proportion of the run that arrives by day t. If this ratio is taken

to be 0.9, for example, then the corresponding day t in equation (5) is called the 90% day for the run. The interested reader can verify from equation (5) that, if $b = -1$, the 50% day is always τ^*. Also, for any value of b, since t equals τ^* minus a term inversely proportional to x', it follows that the entire run is more compressed around the time τ^* for larger peak run proportions x'.

Curve 4 has an important property that enhances its utility as a run curve model. Suppose that fish entering the fishery at time t eventually reach the hatchery at a later time

$$s = \alpha t + \beta.$$

Thus, when $\alpha = 1$, there is a fixed time lag β between the fishery and the hatchery. When $\alpha < 1$, the run into the hatchery is compressed relative to the fishery run, and when $\alpha > 1$ the run is relatively expanded. If $Z(s)$ represents the cumulative run into the hatchery at time s such that

$$(6) \quad Z(s) = X[(s - \beta)/\alpha],$$

then it follows that $Z(s)$ can be represented as the same type of curve as $X(t)$ in equation (4):

$$(7) \quad Z(s) = X_\infty \{1 - b \exp [-z'(1 - b)^{-(1-b)/b} \times (s - \sigma^*)]\}^{1/b}.$$

In equation (7), z' is the peak run proportion per day in the hatchery and σ^* is the peak day on the rate of entry curve $z(s) = dZ/ds$. These parameters are related to x' and τ^* by

$$(8) \quad z' = \alpha^{-1} x'$$

and

$$(9) \quad \sigma^* = \alpha\tau^* + \beta.$$

Equation (7) is a direct consequence of equations (4), (6), (8), and (9). Notice that equation (6) preserves the skewness parameter b and the total run X_∞; the loss of fish in the fishery is considered in the next section. Also, equation (6) is consistent with the simple transformation (9) between peak days, and, from equation (8), the peak run proportion is increased or decreased when the run is compressed ($\alpha < 1$) or expanded ($\alpha > 1$), respectively.

Throughout this section, the skewness parameter b can be positive or negative; however, several equations, such as (1)–(5), are undefined for $b = 0$. In all these cases, there is a continuous extension to $b = 0$. When $b > 0$, there is a theoretical time τ_0 prior to which no fish arrive, that is, $X(t) = 0$ for $t < \tau_0$. Also, when $b > 1$, the parameter τ^* in (1) no longer corresponds to an inflection point. Thus, a natural constraint on the skewness parameter is $b < 1$; in practice, b is usually negative. Technical details in support of this discussion appear in Appendix B, along with formulas for $x(t)$ and $z(t)$.

In an earlier paper, Schnute (1981) stressed the importance of choosing the right parameters in a growth model. This choice, however, depends on the application. Here, the parameter X_∞ is known from historical data, and in general, the cumulative run curve $X(t)$ is known to be asymptotic. Schnute (1981) was concerned with modeling data in which asymptotic growth is not known a priori. Consequently, his parameters are inappropriate here; however, his principle of using biologically meaningful parameters motivates the derivation of equation (4).

Pool Time in the Fishery

Suppose that fish, once in the fishery, remain there for a fixed time τ (unrelated to the peak arrival day τ^*). Let $P(t)$ represent the total number of fish in the fishery pool at time t. Denote the total escapement from the fishery and total catch up to time t by $Y(t)$ and $C(t)$, respectively. The fish in the pool consist of those that have entered the fishery but have neither escaped nor been caught, that is,

$$(10) \quad P(t) = X(t) - Y(t) - C(t).$$

If there is no fishery, that is, if $C(t) = 0$ for all time, then the escapement up to time t consists of all the arrivals up to the earlier time $t - \tau$; that is,

$$(11) \quad Y(t) = X(t - \tau); \quad C(t) = 0.$$

In this case, equation (10) reduces to the simple difference between arrivals up to times t and $t - \tau$:

$$(12) \quad P(t) = X(t) - X(t - \tau); \quad C(t) = 0.$$

The situation is more complex when there is a fishery. Let $y(t) = dY/dt$ and $c(t) = dC/dt$ denote the escapement and catch rates, respectively, at time t. If fish continue to be equally vulnerable to capture while they remain in the pool, then the daily catch $c(t)$ comes uniformly from fish that have entered the pool between times $t - \tau$ and t. To put it another way, fish arriving at time $t - \tau$ are exposed to continual fishing mortality up to time t. It turns out (Appendix C) that

$$(13) \quad y(t) = x(t - \tau) \exp \left\{-\int_{t-\tau}^{t} [c(s)/P(s)]\, ds\right\}.$$

This is the counterpart of equation (11) when C is not identically zero. To grasp equation (13) intuitively, think of the arrivals at time $t - \tau$ being exposed at later times s to an instantaneous mortality $c(s)/P(s)$, the catch rate in proportion to the pool. Fishing mortality continues until these fish leave the fishery at time t.

Equations (10) and (13) involve the four functions of time, X, Y, P, and C, together with their various derivatives and integrals. In principle, equations (10) and (13) should allow one to solve for any two of these functions in terms of the remaining two. For example, it should be possible to find Y and P from X and C. This is called the "forward problem" because it involves computing escapements Y from earlier arrivals X and catches C. A model to simulate the fishery would essentially have to solve the forward problem. Similarly, it should be possible to find X and P from Y and C, that is, to solve the "backward problem." Analysis of historical data involves solving the backward problem to

infer the arrivals X in the fishery from later escapements Y and catches C.

One particular solution to the forward problem, valid when $C = 0$ for all time, is given by equations (11)–(12). Unfortunately, although solutions to the backward and forward problems are possible in principle, they cannot always be represented in closed form as in equations (11)–(12). Instead, iterative computation is usually necessary. From equations (10) and (13) it follows (Appendix C) that

$$(14)\quad P(t) = \int_{-\infty}^{t} \Big(x(s) - c(s) - x(s-\tau) \times \exp\left\{-\int_{s-\tau}^{s} [c(u)/P(u)]du\right\}\Big)ds.$$

This result is an integral equation in P, given x and c. The important thing to notice in equation (14) is that $P(t)$ on the left is expressed in terms of values of P on the right for earlier times $s < t$. Consequently, equation (14) can be used to compute $P(t)$ from earlier values of P, X, and C, as required by the forward problem. Once P is known, Y can then be found from equation (10) in the form

$$(15)\quad Y(t) = X(t) - P(t) - C(t).$$

In short, equations (14) and (15) are the computational basis for a solution to the forward problem. Similarly, it can be shown (Appendix C) that

$$(16)\quad P(t) = \int_{t}^{\infty} \Big(y(s) + c(s) - y(s+\tau) \times \exp\left\{\int_{s}^{s+\tau} [c(u)/P(u)]du\right\}\Big)ds,$$

an equation that describes $P(t)$ in terms of later values of P, Y, and C, as required by the backward problem. Also, from equation (10),

$$(17)\quad X(t) = Y(t) + P(t) + C(t),$$

so that equations (16) and (17) can be used for computing a solution to the backward problem. Notice, incidentally, that in equations (14)–(15) the solution to the forward problem involves subtracting catches, while in equations (16)–(17) the backward problem is solved by adding catches.

Equations (14)–(17) are cast in terms of continuous time t. Practical computation requires discrete time intervals, so that X, Y, P, and C are represented as vectors. The integrals in equations (14) and (16) become sums, indeed finite sums, because c is zero at times before and after the fishery. Additional description of computation appears in the discussion of likelihood below.

The Composite Model

The previous sections include models for the salmon run and the fishery. To complete the description of the terminal fishery, it remains only to include test fishing. Let $U(t)$ represent the test catch per unit effort at time t, and assume that $U(t)$ is proportional to the pool size $P(t)$. This assumption is included in the following composite terminal fishery model:

$$(18)\quad X(t) = X_\infty\{1 - b \exp[-x'(1-b)^{-(1-b)/b} \times (t - \tau^*)]\}^{1/b}$$

$$(19)\quad y(t) = x(t-\tau) \exp\left\{-\int_{t-\tau}^{t} [c(s)/P(s)]\, ds\right\}$$

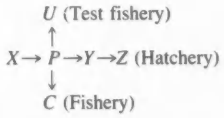
$$(20)\quad P(t) = X(t) - Y(t) - C(t)$$

$$(21)\quad U(t) = qP(t)$$

$$(22)\quad Z(s) = Y[\tau^* + \tau + z'(s - \sigma^*)/x'].$$

The first three of these equations have been given earlier as equations (4), (13), and (10), respectively. The fourth equation asserts that U and P are proportional with a constant of proportionality q (called the catchability coefficient). Finally, equation (22) comes from equations (6), (8), and (9), together with the time lag τ between values of X and Y.

The five equations (18)–(22) completely specify a deterministic version of the terminal fishery model used in this paper. Conceptually, equation (18) describes the run X of fish into the fishery, and equation (19) accounts for the removal of the catch C, leaving an escapement Y. Equation (20) specifies the pool size P as the balance of fish left in the fishery, and equation (21) relates this pool size to the test catch per unit effort. Finally, equation (22) accounts for the time lag between escapement from the fishery and arrival in the hatchery. The flow of fish into the fishery, test fishery, and hatchery follows the simple diagram:



Equations (18)–(22) involve six functions of time (X, Y, Z, C, P, U), three of their derivatives (x, y, c), and eight parameters (X_∞, τ^*, x', b, τ, q, σ^*, and z'). In historical data analysis the total run X_∞ is known, but the seven remaining parameters (seven of the eight cited in the overview) are not. Four more useful parameters include the following:

$$(23)\quad X' = (1 - b)^{1/b}$$

$$(24)\quad \tau_p^* = \tau^* + \tau/2$$

$$(25)\quad \alpha = x'/z'$$

$$(26)\quad t_0 = \tau^* + (s_0 - \sigma^*)/\alpha.$$

The various functions and parameters in equations (18)–(26) have all been discussed earlier, except for quantities in equations (24) and (26). Since τ^* represents the peak day for arrivals in the fishery, it follows from equation (24) that the later time τ_p^* is the peak day for arrivals midpool. The parameters t_0 and s_0 in equation (26) represent corresponding fishery

and hatchery arrival days. If s_0 is a typical day for escapement in the hatchery (arbitrarily chosen by the modeler), then fish reaching the hatchery on day s_0 would have entered the fishery on the earlier day t_0.

The catch C includes the test catch, as well as catch from other fisheries, such as commercial and sport. Typically, the removal of catch distorts the shape of Z from an S curve, and the arrival rate curve z becomes a dome-shaped curve with a portion of the dome removed. Sometimes, removal from the dome makes z appear bimodal because a cut out of the dome leaves a crater. These considerations can be important when interpreting the parameters such as σ^* and z' associated with Z. For example, σ^* is the peak hatchery arrival day if there were no fishing ($C = 0$ for all time), in which case Z would be an S curve of the same type as X. Thus, parameters for Z are used to describe how Z would appear without the terminal fishery. In this case, Z shares the parameters X_∞, b, and X' with X; that is, the total run, the skewness, and the arrival fraction on the peak day are the same in both the fishery and the hatchery.

Likelihood

The overview above shows that a practical version of the model necessarily involves a description of statistical error: the discrepancy between observations and predictions. Two possible sources of error are considered here. First, the incoming run curve $X(t)$ in equation (18) is taken as a probability distribution rather than an exact description. Second, the catch per unit effort $U(t)$ in equation (21) is presumed to contain log normal errors. Both these errors are described in detail below, and the associated likelihood functions are defined precisely.

The analysis requires three data sets. First, there is the daily catch rate $\hat{c}(t)$ known for each time t in the fishery. Second, the test catch per unit effort $\hat{U}_i = \hat{U}(t_i)$ is known for a series of times t_i, $i = 1, \ldots, M$. Finally, the hatchery record gives the daily escapement rate $\hat{z}(s)$ for each time s in the hatchery. In practice, $\hat{c}(t)$ is usually a step function. For instance, suppose that catch takes place only on Julian days 228 and 235 and consists of 5000 and 7000 fish, respectively. Then

$$\hat{c}(t) = 5000 \text{ fish/d}; \quad 228.0 \le t < 229.0$$

$$\hat{c}(t) = 7000 \text{ fish/d}; \quad 235.0 \le t < 236.0$$

$$\hat{c}(t) = 0 \text{ fish/d}; \quad \text{otherwise.}$$

The observed cumulative catch $\hat{C}(t)$ is then piecewise linear; in the example above particular values of $\hat{C}$ are $\hat{C}(228) = 0$ fish, $\hat{C}(228.5) = 2500$ fish, $\hat{C}(229) = 5000$ fish, $\hat{C}(235) = 5000$ fish, $\hat{C}(235.5) = 8500$ fish, etc. Similar remarks apply to $\hat{z}$ and $\hat{Z}$. This method of linear interpolation for cumulative functions such as $\hat{C}$ and $\hat{Z}$ facilitates computation by allowing discrete data to be regarded as continuous functions of time.

To describe the likelihood function for the data $\hat{c}(t)$, $\hat{z}(s)$, and $\hat{U}(t_i)$, $i = 1, \ldots, M$, the seven preliminary steps below are required.

Step 1 — From $\hat{c}(t)$ and $\hat{z}(s)$ compute $\hat{C}(t)$ and $\hat{Z}(s)$ as above. If t_f and s_f are days in the fishery and hatchery beyond which there is no further catch and escapement, respectively, then define

$$X_\infty = \hat{C}(t_f) + \hat{Z}(s_f), \tag{27}$$

the observed total run.

Step 2 — Choose two times s_a and s_b near the beginning and end, respectively, of the observed hatchery run $\hat{Z}(s)$, and choose a number N associated with the step size

$$\Delta s = (s_b - s_a)/(N - 2).$$

Then s_a, s_b, and N determine the N time intervals

$$(-\infty, s_a), (s_a, s_a + \Delta s), \ldots, (s_b - \Delta s, s_b), (s_b, \infty),$$

which, in turn, distinguish N groups of fish arriving in the hatchery during each interval. These groups yield multinomial probabilities used in defining the likelihood associated with a smooth run curve, when the curve is interpreted as a probability distribution. Choose s_a and s_b so that the left and right intervals, respectively, correspond to a small fraction (e.g. 0.1−1%) of the total hatchery arrivals $\hat{Z}(s_f)$, and choose N so that the middle interval corresponds to a moderate fraction (e.g. 5−10%) of total arrivals.

Step 3 — Choose a fixed day s_0 near the middle of the hatchery run $\hat{Z}(s)$. The likelihood function will depend in part on the seven parameters α, t_0, τ, q, τ^*, x', and b in equations (18)−(26), as well as X_∞ defined by equation (27).

Step 4 — For given values of α, t_0, and τ, determine the function

$$\hat{Y}(t;\alpha,t_0,\tau) = \hat{Z}[s_0 + \alpha(t - t_0 - \tau)]. \tag{28}$$

This corresponds to the escapement $\hat{Y}$ from the fishery, which would explain the arrivals $\hat{Z}$ in the hatchery, as defined by equations (22), (25), and (26). In equation (28), the dependence of $\hat{Y}$ on three parameters is emphasized.

Step 5 — From the functions $\hat{Y}$ and $\hat{C}$, solve the backward problem for equations (19)−(20) to obtain the functions

$$\hat{X} = \hat{X}(t;\alpha,t_0,\tau), \quad \hat{P} = \hat{P}(t;\alpha,t_0,\tau), \tag{29}$$

that is, the fishery arrivals $\hat{X}$ and pool sizes $\hat{P}$, which would account for the escapements $\hat{Y}$ and catch $\hat{C}$.

Step 6 — For given values of τ^*, x', and b compute

$$X = X(t;\tau^*,x',b) \tag{30}$$

from equation (18), that is, the exact run curve determined by these parameters. In equation (30) the parameter X_∞ is not shown because it is determined from the data by equation (27) and will not be allowed to vary.

Step 7 — Define $\hat{X}_0 = 0$, $\hat{X}_N = X_\infty$, and

$$(31)\quad \hat{X}_j = \hat{X}[t_0 + (s_a - s_0)/\alpha + (j-1)\,\Delta s/\alpha]; \qquad j = 1, \ldots, N-1.$$

Then define

$$(32)\quad \hat{A}_j(\alpha,t_0,\tau) = \hat{X}_j - \hat{X}_{j-1};\quad j = 1, \ldots, N,$$

where $\hat{A}_j$ depends on α, t_0, and τ through equations (29) and (31). Similarly, define $X_0 = 0$, $X_N = X_\infty$,

$$(33)\quad X_j = X[t_0 + (s_a - s_0)/\alpha + (j-1)\,\Delta s/\alpha]; \qquad j = 1, \ldots, N-1,$$

and

$$(34)\quad A_j(\tau^*,x',b,\alpha,t_0) = X_j - X_{j-1};\quad j = 1, \ldots, N,$$

where A_j depends on τ^*, x', and b through equation (30) and on α and t_0 through equation (33). Conceptually, $\hat{A}_j$ and A_j for $j = 1, \ldots, N$ represent the actual and theoretical numbers of fish that arrive in the fishery for each of the N groups described in step 2 above.

Once the above steps are completed, the likelihood function can be described in terms of $\hat{P}(t)$, $\hat{A}_j$, and A_j ($j = 1, \ldots, N$) in equations (29), (32), and (34), respectively. The function has two components, due to test fishing and the run curve. To obtain the test fishing component, assume log normal errors in equation (21), that is,

$$(35)\quad \hat{U}(t_i) = q\hat{P}(t_i)\exp(\gamma\epsilon_i);\quad i = 1, \ldots, M,$$

where the ϵ_i are independent normal errors with mean 0 and variance 1. In equation (35), the new parameter γ represents a standard deviation associated with the log normal errors. The likelihood function connected with equation (35) is

$$(36)\quad L_1(q,\gamma,\alpha,t_0,\tau) = (2\pi)^{-M/2}\gamma^{-M} \times \exp\left\{-\sum_{i=1}^{M}[\log(q\hat{P}_i/\hat{U}_i)/(2\gamma)]^2\right\},$$

where $\hat{P}_i$ and $\hat{U}_i$ represent $\hat{P}(t_i)$ and $\hat{U}(t_i)$, respectively. The run curve component comes from the multinomial distribution applied to the N groups of fish in steps 2 and 7 above, that is,

$$(37)\quad L_2(\tau^*,x',b,\alpha,t_0,\tau) = X_\infty!\prod_{j=1}^{N}[(A_j/X_\infty)^{\hat{A}_j}/\hat{A}_j!].$$

Given values of the three parameters α, t_0, and τ, the estimates $\hat{q}$ and $\hat{\gamma}$ that maximize L_1 in equation (36) turn out to satisfy

$$(38)\quad \hat{q}(\alpha,t_0,\tau) = \left[\prod_{i=1}^{M}(\hat{U}_i/\hat{P}_i)\right]^{1/M}$$

and

$$(39)\quad \hat{\gamma}^2(\alpha,t_0,\tau) = M^{-1}\sum_{i=1}^{M}[\log(\hat{q}\hat{P}_i/\hat{U}_i)]^2.$$

At these optimal estimates for q and γ, the negative logarithm of the likelihood L_1 becomes (Appendix D)

$$(40)\quad \ell_1(\alpha,t_0,\tau) = M\log\hat{\gamma}(\alpha,t_0,\tau),$$

except for a constant independent of the parameters.

The negative logarithm of the likelihood L_2 can be written as a sum of two terms (Appendix D)

$$(41)\quad \ell_2(\tau^*,x',b,\alpha,t_0,\tau) = \ell_{2a}(\tau^*,x',b,\alpha,t_0,\tau) + \ell_{2b}(\alpha,t_0,\tau),$$

where

$$(42)\quad \ell_{2a}(\tau^*,x',b,\alpha,t_0,\tau) = \sum_{j=1}^{N}\hat{A}_j\log(\hat{A}_j/A_j)$$

and

$$(43)\quad \ell_{2b}(\alpha,t_0,\tau) = \sum_{j=1}^{N}[\log(\hat{A}_j!) - \hat{A}_j\log(\hat{A}_j) + \hat{A}_j].$$

In equations (41)–(43), constants independent of parameters have again been ignored; the dependence on various parameters follows from equations (32) and (34). The function ℓ_{2a} is a well-known information function associated with frequency data (Rao 1973; Schnute and Fournier 1980); it is always positive and takes the minimum value 0 only if the actual counts $\hat{A}_j$ agree exactly with the predicted counts A_j for each j. The function ℓ_{2b} ordinarily does not enter the analysis of frequency data because it depends only on the actual counts $\hat{A}_j$. In the present context, however, the actual counts themselves depend on certain parameters as a result of the back-calculation from $\hat{Z}$ to $\hat{X}$. It turns out that the practical influence of ℓ_{2b} is small because ℓ_{2b} typically is much less than ℓ_{2a}.

Ultimately, the historical analysis of test fishery data boils down to finding parameters that minimize ℓ_1 and ℓ_2. In particular, three problems hold special interest.

Problem 1 — Find parameter estimates $\hat{\alpha}$, $\hat{t}_0$, and $\hat{\tau}$ that minimize $\ell_1(\alpha,t_0,\tau)$. This corresponds to finding the timing parameters between fishery and hatchery that give the best explanation of the test fishery data.

Problem 2 — Suppose that the parameters σ^*, z', and b are known for the arrivals Z in the hatchery. Then, given α and t_0, the corresponding parameters τ^*, x', and b for arrivals X in the fishery can be computed; in particular, from equations (25) and (26)

$$\tau^* = t_0 + (\sigma^* - s_0)/\alpha;\quad x' = \alpha z'.$$

Consequently, ℓ_2 becomes a function of α, t_0, and τ alone; the problem is to find estimates $\hat{\alpha}$, $\hat{t}_0$, and $\hat{\tau}$ that minimize ℓ_2. This corresponds to finding timing parameters that best explain the fishery arrivals X as a smooth run curve consistent with a prescribed hatchery run curve.

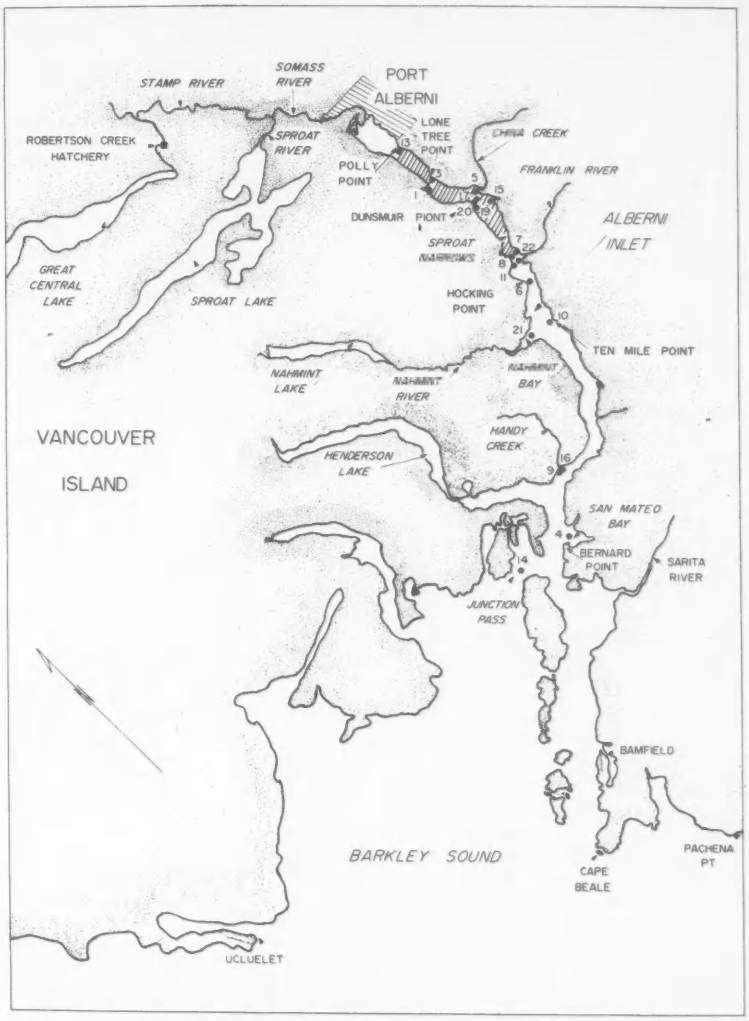


FIG. 2. Study area showing test fishery sites (solid circles, numbered). The commercial fishing area (cross-hatched) includes approximately an 11.5-km length of Alberni Inlet. Approximate coordinates for Port Alberni are 49°N latitude and 125°W longitude.

Problem 3 — Let W be a prescribed weight factor that determines the relative importance of (i) fitting test fishery data and (ii) describing fishery arrivals X by means of a smooth run curve. Find parameter estimates $\hat{\tau}^*$, $\hat{x}'$, $\hat{b}$, $\hat{\alpha}$, $\hat{t}_0$, and $\hat{\tau}$ that minimize the composite negative log−likelihood:

$$(44) \quad \ell(\tau^*, x', b, \alpha, t_0, \tau) = W\ell_1 + \ell_2.$$

This corresponds to finding both timing and run curve parameters that give the best overall explanation of the observed data, given the subjective weight factor W.

The solution to any of the above problems also gives the estimates $\hat{q}$ and $\hat{\gamma}$ in equations (38) and (39), as well as estimated fishery arrivals $\hat{X}$, pool sizes $\hat{P}$, and escapements $\hat{Y}$, in short, a complete construction of the run of fish and the fishery. By comparing arrivals $\hat{X}$ with escapements $\hat{Y}$, one can infer the precise portion of the run from which the catch was

TABLE 1. Summary of Alberni Inlet chinook adult run, 1978–81.

	1978	1979	1980	1981	Total
Catch					
Commercial	9 993	12 762	26 265	27 480	76 500
Food, sport	4 921	9 765	9 729	10 002	34 417
Test	972	1 164	953	599	3 688
Total	15 886	23 691	36 947	38 081	114 605
Escapement					
Hatchery	13 995	21 069	20 525	17 562	73 151
Wild	8 000	3 840	4 000	6 500	22 340
Total	21 995	24 909	24 525	24 062	95 491
Total run	37 881	48 600	61 472	62 143	210 096

taken. In practice, both problems 1 and 2 typically have multiple solutions, as described in the example below. Fortunately, there tend to be few overlapping solutions; these are singled out by solving problem 3. Even problem 3 may have more than one solution, and the modeler is forced to accept or reject a solution based on subjective criteria applied to the details of run reconstruction. Again, this is illustrated in the example below.

It turns out that ℓ_1 and ℓ_2 are continuous, but not differentiable, functions of their parameters. For this reason, the functions are best minimized by a direct search algorithm, such as the simplex method (Nelder and Mead 1965; O'Neill 1971; Schnute 1982). The six-dimensional search for a minimum to problem 3 is much assisted by a preliminary look at contours for the two three-dimensional functions involved in solving problems 1 and 2.

Example

Alberni Inlet Chinook Fishery

Although the model presented in this paper could be applied to most salmon terminal fisheries, it was designed particularly to study the chinook (*Oncorhynchus tshawytscha*) fishery in Barkley Sound and the Alberni Inlet on the southwest coast of Vancouver Island, British Columbia, Canada. Figure 2 shows the relevant geography. Chinook smolts come from the hatchery at Robertson Creek, which is about 20 km from tide water on a tributary of the Stamp River, the outflow from Great Central Lake. The Stamp is a tributary to the Somass, which enters Alberni Inlet near the city of Port Alberni. In addition to hatchery stocks, the Somass system supports a number of wild stocks, particularly in the Stamp and Sproat rivers. A dam on the Stamp regulates the flow regime of the Somass.

Alberni Inlet is a long (50 km) narrow (1–2 km) fjord, which contains the estuary of the Somass River. The Inlet connects to the Pacific Ocean through Barkley Sound, a protected body of water containing many islands. A sport fishery occurs throughout the system from Barkley Sound to Port Alberni. A commercial gillnet fishery is allowed between Sproat Narrows and Polly Point in Alberni Inlet (cross-hatched region in Fig. 2). A native food fishery occurs in the lower 1–2 km of the Somass River. During the chinook run, test fishing is conducted at various points in the Inlet and Sound, as indicated by solid circles and location codes in Fig. 2.

TABLE 2. Summary of the duration and extent of test fishing for chinook in the Alberni Inlet, 1978–81.

	1978	1979	1980	1981	Average
First day (Julian)	227	225	217	223	223.0
Last day (Julian)	298	252	257	245	263.0
No. of sets	82	30	36	27	43.8

Robertson Creek Hatchery began releasing chinook smolts in 1972, and the first returns to contain 3-, 4-, and 5-yr-old fish occurred in 1977. Commercial fishing has been allowed since 1978, and the analysis here covers the 4-yr period 1978–81 during which an annual test fishery also took place. The analysis is based on adults alone (age 3–6), since jacks (age 2) have distinctly different run timing; they are also less vulnerable to the fishery and have relatively little economic value.

Data

The majority of catch is taken by the commercial fishery, and the total catch on each commercial fishing day is monitored and recorded, both for adults and jacks. The sport and Indian food fisheries are more difficult to monitor, and data are usually available on a weekly basis at best. For the purposes of analysis here, adult catch data from all sources are compiled on a daily basis by distributing, for example, weekly catches over the days of the week. This introduces a potential error in timing estimates, but the error should be small because the noncommercial catches per week are relatively small.

The test fishery was conducted by a chartered commercial gillnetter. Sets were typically conducted at night with about a 2-h soak time. A variety of data were collected for each fish caught in the test fishery, such as hypural length, sex, and age based on scale reading. The analysis here uses the adult catch per hour for each set as the measure of catch per unit effort. More sophisticated analyses might be possible to take account of conditions of moon and tide, as well as location, but these extra factors were recorded erratically over the period 1978–81.

Hatchery records are the primary source of escapement data. These consist of daily or bidaily counts of returning

fish captured in the brailer at the Robertson Creek Hatchery. Escapements of wild stocks to other components of the Somass system are estimated occasionally during the run by Fisheries Officers in Port Alberni. The accuracy of these estimates is unknown, and they are not done with sufficient frequency to infer timing; however, available data do not conflict with the hypothesis that the timing is the same as that of the Robertson Creek component. The principal wild stock measurements come from the Stamp and Sproat rivers, and only the Stamp was examined in all 4 yr, 1978–81. The analysis here is based on the Robertson Creek records increased proportionally to include wild stock in the Stamp. This introduces two potential errors: neglect of non-Stamp stocks and Stamp versus Robertson Creek timing differences. Both of these problems probably have little influence on the results of this analysis; indeed, the results do not change much even if the wild Stamp escapement is ignored.

Table 1 summarizes the numbers of fish involved in all aspects of the analysis. Over the period of interest, the run increases and leads to a greater available harvest of fish. Table 2 summarizes the duration and extent of the test fishery in each year from 1978 to 1981. Notice that the most extensive test fishing took place in 1978, while the 1981 test fishery covered the shortest time period and included the fewest sets.

Results

To gain preliminary insight into the arrival time of adult chinook in the hatchery, one can simply calculate the days when, for example, 10, 50, and 90% of the fish have arrived. The peak day, that is, the day when the most fish were counted in the brailer, is also of interest. A similar calculation can be applied to the test catch to gain insight into the arrival time in the fishery, although this calculation must be interpreted carefully because it depends critically on when test fishing happens to have been carried out. Table 3 summarizes the results of these calculations. (Throughout this discussion, days are reported as Julian calendar days.) It appears that the 1978 run lasted longer in the fishery than later runs, but from Table 2, that could easily be an artifact of the decision to conduct shorter test fisheries in 1979–81. The run into the hatchery exhibits remarkable consistency over the period; in particular, the 50% day turns out to be either Julian day 295 or 296 (October 22 or 23). The apparent peak day varies somewhat from year to year, but that can be explained by random variation in the daily brailer counts; similarly, the apparent fishery peak day depends on an erratic test catch.

Table 4 is based on finding the optimal run curve (4) for the hatchery escapement data, where "optimal" refers to the curve with the lowest value for ℓ_{2a}. In equation (4) the three key parameters are τ^* (peak day), x' (peak percent per day), and b (skewness). Once these are known, the 10, 50, and 90% days can be computed from equation (5); also, the parameters X' (percent at peak) and a can be computed from equations (2) and (3), respectively. Table 4 demonstrates three important features of the run into the hatchery. First, the estimated 10, 50, and 90% days and peak days agree quite well with the preliminary estimates in Table 3; consequently, equation (4) appears to be a reasonable model for the data. Second, all the various parameter estimates are highly consistent from year to year, suggesting great predictability in run timing. Third, the skewness parameter b is the least consistent. In 1978–80, the peak day precedes the 50% day, so that the run is skewed left ($b > -1$, $X' < 50\%$, and $\tau^* < t_{50\%}$), while in 1981 the run is skewed right ($b < -1$).

The analysis in Table 4 does not account for the catch removed from the run before the fish reach the hatchery. The full model described above is needed to estimate timing in both the hatchery and fishery so that catch can be appropriately included. Unfortunately, the resulting estimation

Table 3. Timing data for Alberni Inlet chinook adults, 1978–81, based on raw data from the test fishery and hatchery.

	1978	1979	1980	1981	Average
Test fishery					
10% day	232	229	225	231	229.3
50% day	243	241	235	235	238.5
90% day	265	245	249	243	250.5
Peak day	240	246	249	243	244.5
Hatchery					
10% day	285	289	285	284	285.8
50% day	296	296	295	295	295.5
90% day	306	308	307	305	306.5
Peak day	296	292	294	297	294.8

Table 4. Best parameters for the Alberni chinook adult run, 1978–81, based on hatchery escapement data alone.

	1978	1979	1980	1981	Average
Hatchery					
10% day	287.83	289.57	286.42	285.87	287.42
50% day	296.73	297.82	296.72	296.92	297.05
90% day	307.29	309.75	307.94	306.69	307.92
Peak day	295.93	295.90	296.28	297.50	296.40
% at peak	45.51	39.57	47.77	53.07	46.48
Peak % per day	5.61	5.52	5.07	5.36	5.39
a	0.20	0.16	0.19	0.24	0.20
b	−0.58	−0.16	−0.78	−1.35	−0.72
Likelihood ℓ_{2a}	1820.16	2695.05	3010.22	2200.26	2431.42

TABLE 5. Best parameters for the Alberni chinook adult run, 1978–81, with pool times of 5, 10, 20, and 30 d.

	A. 5-d pool time					B. 10-d pool time				
	1978	1979	1980	1981	Average	1978	1979	1980	1981	Average
Fishery										
10% day	227.46	225.96	225.49	218.18	224.27	205.70	222.19	223.02	211.37	215.57
50% day	250.82	240.69	241.59	237.49	242.65	240.29	236.52	238.80	235.63	237.81
90% day	272.95	259.65	259.64	255.92	262.04	264.95	255.00	256.58	255.26	257.95
Peak day	251.38	238.59	240.65	237.90	242.13	244.52	234.44	237.84	237.65	238.62
Midpool										
10% day	229.96	228.46	227.99	220.68	226.77	210.70	227.19	228.02	216.37	220.57
50% day	253.32	243.19	244.09	239.99	245.15	245.29	241.52	243.80	240.63	242.81
90% day	275.45	262.15	262.14	258.42	264.54	269.95	260.00	261.58	260.26	262.95
Peak day	253.88	241.09	243.15	240.40	244.63	249.52	239.44	242.84	242.65	243.62
% at peak	51.35	43.19	47.02	51.18	48.18	58.28	43.11	46.90	55.21	50.87
Peak % per day	2.43	3.25	3.20	2.93	2.95	1.98	3.34	3.25	2.59	2.79
a	0.10	0.11	0.12	0.12	0.11	0.10	0.11	0.12	0.12	0.11
b	−1.14	−0.40	−0.71	−1.13	−0.85	−2.09	−0.40	−0.70	−1.62	−1.20
Hatchery										
10% day	287.46	290.33	287.39	289.96	288.79	289.40	290.65	287.51	290.87	289.61
50% day	296.04	298.64	296.24	299.67	297.64	299.10	299.70	296.71	299.70	298.80
90% day	304.17	309.34	306.15	308.92	307.15	306.01	311.37	307.09	306.84	307.83
Peak day	296.24	297.45	295.72	299.87	297.32	300.29	298.39	296.16	300.43	298.82
% at peak	51.35	43.19	47.02	51.18	48.18	58.28	43.11	46.90	55.21	50.87
Peak % per day	6.61	5.76	5.82	5.82	6.01	7.05	5.29	5.57	7.11	6.25
a	0.28	0.19	0.21	0.24	0.23	0.37	0.17	0.20	0.34	0.27
b	−1.14	−0.40	−0.71	−1.13	−0.85	−2.09	−0.40	−0.70	−1.62	−1.20
Transition										
α	0.37	0.56	0.55	0.50	0.50	0.28	0.63	0.58	0.36	0.46
s_0	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00
t_0	261.61	243.10	248.44	238.16	247.83	243.50	237.00	244.43	236.47	240.35
Pool										
τ	5.00	5.00	5.00	5.00	5.00	10.00	10.00	10.00	10.00	10.00
Peak day %	12.09	16.13	15.85	14.53	14.65	19.47	32.28	31.45	25.25	27.11
q (10^{-3})	1.65	2.08	2.66	0.82	1.80	1.21	1.01	1.21	0.50	0.98
γ	0.87	1.21	0.72	1.55	1.09	0.74	1.17	0.74	1.56	1.05
90% factor	3.06	4.74	2.51	7.27	4.39	2.58	4.46	2.57	7.35	4.24
95% factor	5.52	10.79	4.09	20.76	10.29	4.25	9.82	4.24	21.09	9.85
Likelihood										
ℓ_1	−11.27	5.81	−11.92	11.79	−1.40	−24.92	4.60	−10.96	11.93	−4.84
ℓ_{2a}	2807.84	4996.76	3243.55	4536.16	3896.08	2389.96	4096.14	2909.34	2182.19	2894.41
ℓ_{2b}	54.33	61.93	61.75	71.74	62.44	53.92	60.42	62.08	69.60	61.51
ℓ	−519.13	6802.02	−271.09	8143.94	3538.94	−5032.90	5536.36	−317.24	5830.37	1504.15

problem does not have a single clear solution. As suggested earlier, problem 1 has multiple solutions; that is, there are many possible timing explanations of the test fishery data. Problem 2 can be defined by requiring that escapement timing parameters should conform to those of Table 4; this also leads to multiple solutions (i.e., many possible fishery arrival curves (4)). The relatively few overlapping solutions to problems 1 and 2 make good beginning points in the search for a solution to problem 3, and all such initial points have been attempted in this analysis. Even then, it becomes clear that the pool time τ is poorly determined by the data; consequently, the best approach is to select a few fixed pool times and look for the optimal solution in each case. To balance the likelihood contributions from ℓ_1 and ℓ_2, the weight factor $W = 300$ in equation (44) works well in all cases and solutions are robust to this choice. Table 5 reports the results of this entire analysis for chosen pool times of 5, 10, 20, and 30 d, respectively. Each solution corresponds to the lowest value ℓ found for the given pool time and year, although other local minima of ℓ may exist.

As described earlier, the nonlinear search leading to the results in Table 5 is based on the six parameters τ^*, x', b, α, t_0, and τ. All other parameters can be found once these are known. Some of these parameters, such as the fishery peak day τ^* and the various percentage days, have already been discussed, but others have not. For example, the "midpool" percentage days correspond to their "fishery" counterparts plus $\tau/2$, that is, the day when a given percent of the fish have arrived in the middle of the pool. The midpool peak day τ_p^* is similarly defined in equation (24). The percent arrival at the peak day (X') is the same for both fishery and midpool runs, with the understanding that the peak day is different in each case. Similarly, the fishery and midpool runs share values of x' (peak percent per day), a, and b. The hatchery run also shares fishery values of b and X', but the hatchery values of a and x' are influenced by the run expansion factor α. For example, when $\alpha < 1$ and the run is compressed, then both a and the peak percent per day are increased in the hatchery. The fixed day s_0 is set to be Julian day 300 here, so that t_0 is the day when fish, destined to reach the hatchery on day 300, would arrive in the fishery. It is important to recognize that the hatchery parameters describe the run with the catch added

TABLE 5. (*Concluded*)

	C. 20-d pool time					D. 30-d pool time				
	1978	1979	1980	1981	Average	1978	1979	1980	1981	Average
Fishery										
10% day	192.91	212.28	220.53	218.56	211.07	204.48	198.20	219.43	209.86	207.99
50% day	232.87	230.27	234.17	234.93	233.06	231.41	226.78	230.82	228.87	229.47
90% day	259.85	252.17	249.94	251.57	253.38	253.64	260.71	243.46	246.23	251.01
Peak day	238.37	228.35	233.15	234.81	233.67	233.47	224.19	230.23	229.61	229.38
Midpool										
10% day	202.91	222.28	230.53	228.56	221.07	219.48	213.20	234.43	224.86	222.99
50% day	242.87	240.27	244.17	244.93	243.06	246.41	241.78	245.82	243.87	244.47
90% day	269.85	262.17	259.94	261.57	263.38	268.64	275.71	258.46	261.23	266.01
Peak day	248.37	238.35	243.15	244.81	243.67	248.47	239.19	245.23	244.61	244.38
% at peak	59.63	44.77	46.23	49.59	50.05	54.73	45.48	47.32	52.26	49.95
Peak % per day	1.78	2.74	3.71	3.32	2.89	2.30	1.75	4.54	3.05	2.91
a	0.10	0.09	0.13	0.13	0.11	0.11	0.06	0.17	0.13	0.12
b	−2.32	−0.53	−0.65	−0.96	−1.11	−1.56	−0.58	−0.74	−1.25	−1.03
Hatchery										
10% day	289.60	291.42	286.57	286.93	288.63	288.86	291.73	286.02	288.53	288.78
50% day	299.81	300.07	296.85	296.08	298.20	298.30	299.06	296.73	297.63	297.93
90% day	306.71	310.61	308.72	305.38	307.85	306.10	307.77	308.61	305.94	307.10
Peak day	301.22	299.15	296.08	296.01	298.12	299.03	298.40	296.17	297.99	297.90
% at peak	59.63	44.77	46.23	49.59	50.05	54.73	45.48	47.32	52.26	49.95
Peak % per day	6.95	5.69	4.93	5.95	5.88	6.56	6.81	4.83	6.38	6.14
a	0.39	0.19	0.18	0.23	0.25	0.31	0.24	0.18	0.27	0.25
b	−2.32	−0.53	−0.65	−0.96	−1.11	−1.56	−0.58	−0.74	−1.25	−1.03
Transition										
α	0.26	0.48	0.75	0.56	0.51	0.35	0.26	0.94	0.48	0.51
s_0	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00	300.00
t_0	233.61	230.11	238.36	241.95	236.01	236.25	230.44	234.30	233.82	233.70
Pool										
τ	20.00	20.00	20.00	20.00	20.00	30.00	30.00	30.00	30.00	30.00
Peak day %	33.88	50.04	63.26	58.17	51.34	59.31	48.20	87.98	72.09	66.89
q (10^{-3})	0.68	0.61	0.58	0.25	0.53	0.37	0.63	0.39	0.16	0.39
γ	0.69	1.19	0.71	1.49	1.02	0.69	1.20	0.72	1.44	1.01
90% factor	2.42	4.60	2.49	6.72	4.06	2.42	4.66	2.51	6.31	3.97
95% factor	3.86	10.31	4.04	18.40	9.15	3.86	10.53	4.08	16.71	8.79
Likelihood										
ℓ_1	−30.46	5.23	−12.20	10.69	−6.68	−30.54	5.50	−11.97	9.78	−6.81
ℓ_{2a}	1845.23	2621.78	4523.58	4504.83	3373.86	2356.14	1963.73	4647.09	3538.99	3126.49
ℓ_{2b}	54.00	57.93	62.59	70.99	61.38	54.30	53.98	63.56	69.50	60.34
ℓ	−7239.79	4248.71	927.58	7783.54	1430.01	−6752.97	3667.51	1119.65	6543.59	1144.44

back in; thus, they predict how the hatchery run might have been without the fishery.

The pool peak day percent is defined from the peak day fraction:

$$X_\infty^{-1}\,[X(\tau^* + \tau/2) - X(\tau^* - \tau/2)].$$

Assuming no fishing, this is the projected pool size on the midpool peak day in relation to the whole run. For technical reasons, unless $b = -1$, this is nearly, but not quite exactly, the maximum fraction of the run ever in the pool (without fishing).

Because a unit of effort here is a gillnet-hour, q can be interpreted as the fraction of the pool that would be removed in an hour of gillnet fishing. Two error factors can be associated with the standard error γ:

$$90\%\ \text{factor} = e^{1.282\gamma}$$

$$95\%\ \text{factor} = e^{1.960\gamma}$$

where 1.282 and 1.960 are 90 and 95% confidence limits, respectively, for a normal distribution with SD = 1. Theoretically, 90% of the time, the observed catch per unit effort $\hat{U}$ should be within the 90% factor of the predicted value $\hat{q}\hat{P}$.

Table 5 allows one to examine how various parameter estimates vary with prescribed pool times and years. It may happen that an estimate depends little on the pool time, the year, or both. Consistency among years is particularly important because it suggests a predictable feature in the run. Independence from pool time is also useful, since the pool time itself is so ill-conditioned. These considerations and the data in Table 5 lead to the following conclusions:

1) Fishery arrival times depend on the presumed pool time much more than midpool arrival times. Longer pool times are consistent with earlier arrivals in the fishery.
2) For $\tau \geq 10$, the midpool 50% day is particularly well determined, independent of the year, to lie between day 240 and 245. For 1980–81, this is somewhat later than the time suggested in the preliminary analysis in Table 3 based solely on the test fishery.
3) The hatchery peak day, 50% day, and 90% day are all

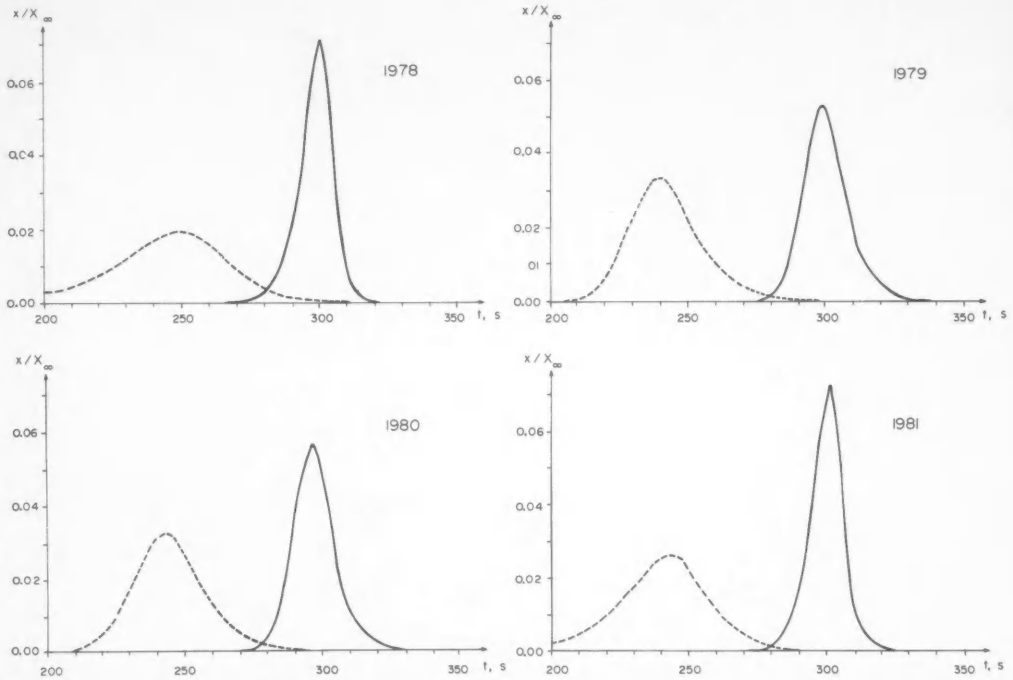


FIG. 3. Estimated daily run into the fishery (broken curve) and hatchery (solid curve) for the example worked in this paper, assuming a 10-d pool time. The four panels for 1978–81 represent the result of four independent analyses based on data collected for each year. The horizontal axis indicates the Julian day, and the vertical axis indicates the fraction of the total run arriving per day. Parameters used to generate these curves appear in Table 5 (10-d pool time).

quite well determined independent of pool time or year. Both the peak day and the 50% day appear to be later in Table 5 than in the preliminary estimates of Table 4. Thus, the model predicts that the hatchery runs in 1978–81 would have included more fish coming slightly later if there had been no fishery.

4) The skewness parameter b is rather independent of pool time, but varies from year to year. Adding the catch to the 1978 run changes its apparent skewness from left to right in comparison with the preliminary estimate in Table 4.
5) The run expansion factor α depends somewhat both on the choice of pool time and year. However, the model is definite in its prediction that $\alpha < 1$: the run contracts during migration to the hatchery. This means that the dome-shaped curve describing the fishery run is lower and more spread out than its counterpart curve in the hatchery. Typically, between 2 and 4% of the total run arrives in the fishery on the peak day, while between 5 and 7% of the run reaches the hatchery on the peak day. The arrival period for the middle 80% of the run (difference between 90% day and 10% day) is between 30 and 50 d in the fishery but only 15–25 d in the hatchery. These data are consistent with α equal to about 0.5. Figure 3 illustrates the run curves for each year of 1978–81 associated with a 10-d pool time (the parameters of Table 5B).
6) The value of q distinctly depends on the pool time. This is not surprising, since the larger the pool time, the bigger the pool and the smaller the pool proportion represented by a given test catch. Except for 1981, the value of q is remarkably consistent among years. Furthermore, by far the worst fit to the test data (largest γ) happens in 1981, so it is reasonable to give the 1981 estimate for q least credence. Averages of q for 1978–80 follow the schedule:

τ	q (10^{-3})
5	2.13
10	1.14
20	0.62
30	0.46

In future years, this schedule might guide a manager in estimating the pool size from the test catch, based on a prior concept of the pool time.

7) Similarly, the percent of the total run in the pool on the midpool peak day depends more on the pool time than the

TABLE 6. A partial 1980 list of observed catches and predicted pool sizes corresponding to four pool times, along with the percent removal that each catch represents. The early and late small catches at the top and bottom of the table, respectively, comprise only sport and food catch. Each 1980 commercial fishing day is included in the middle group, and the line of averages applies to this group.

		$\tau = 5$		$\tau = 10$		$\tau = 20$		$\tau = 30$	
Day	Catch	Pool	%	Pool	%	Pool	%	Pool	%
215	71	377	19	666	11	1 140	6	1 458	5
220	122	991	12	2 106	6	4 269	3	6 467	2
232	5113	9 860	52	15 279	33	26 862	19	35 584	14
233	2100	6 217	34	12 372	17	23 934	9	32 200	7
238	6135	11 668	53	16 722	37	29 033	21	35 902	17
239	2406	6 953	35	11 773	20	23 789	10	31 254	8
244	5764	8 670	66	12 699	45	22 877	25	37 281	15
252	5248	7 491	70	9 909	53	20 926	25	30 641	17
Average	4461	8 477	52	13 126	34	24 570	18	33 810	13
260	103	3 003	3	6 394	2	11 187	1	15 316	1
270	211	1 776	12	1 972	11	3 264	6	6 222	3

TABLE 7. Reconstructed 1980 Alberni chinook adult run, assuming a 10-d pool time. Escapements include wild stock, allocated in proportion to observed counts at the hatchery. The added catch results from solving the backward problem using transition parameters in Table 5B; similarly, the expected run comes from hatchery parameters in Table 5B.

Arrival day					
Fishery	Hatchery	Escapement	Catch	Total	Expected
196.43	272	80	313	393	95
201.57	275	287	105	392	128
206.72	278	5	4	9	295
211.86	281	198	327	525	661
217.00	284	315	270	586	1 424
222.14	287	1 722	531	2 253	2 855
227.29	290	2 840	2 306	5 146	5 125
232.43	293	3 047	6 533	9 580	7 851
237.57	296	3 462	8 673	12 135	9 856
242.72	299	2 973	4 687	7 660	9 984
247.86	302	2 058	4 563	6 620	8 307
253.00	305	1 832	3 804	5 636	5 920
258.14	308	3 084	1 589	4 673	3 788
263.29	311	2 367	1 511	3 878	2 264
268.43	314	124	358	483	1 299
273.57	317	80	619	699	729
∞	∞	51	752	803	892
Total		24 525	36 947	61 472	61 472

year. Notice that in 1980, assuming a 30-d pool time, about 88% of the whole run would be in the pool that day.

8) Although the minimum value of ℓ does not vary greatly among pool times, the actual minimum for each year of 1978–81 is achieved at $\tau = 20$, 30, 10, and 10, respectively. For all years, a pool time of 10 d gives a lower ℓ than a time of 5 d.

The above conclusions illustrate the model's description of the fishery from the viewpoint of optimal parameters. In addition, each solution in Table 5 corresponds to a detailed reconstruction of the run. In some cases, these details help resolve apparent ambiguities based on looking at the parameters alone. To illustrate, consider the 1980 run; unlike other years, 1980 had both large commercial catches and a reasonably extensive test fishery (Tables 1 and 2). Table 6 shows detailed catches and pool sizes on various days, including all days of commercial fishing, for each of the four pool times in Table 5. Notice that larger pool times correspond to larger pools and smaller percent removals by the fishery. The manager may have some feeling for the fraction of available fish that the commercial fishery can take in a day. If so, then Table 6 suggests an appropriate pool time; for instance, a pool time of 10 d is consistent with a typical daily removal of about one third of the pool. A long pool time such as 30 d

TABLE 8. Observed adult catch per unit effort $\hat{U}$ for each set in the 1980 Alberni chinook test fishery. Expected catch per unit effort, U, is also given, based on the run reconstruction with a 10-d pool time. The error factor indicates the multiplicative error in $\hat{U}$ as a predictor of U. It is labeled negative when $\hat{U}$ underestimates U. Thus, the factor is either $\hat{U}/U$ or $-U/\hat{U}$.

Day	Set	Pool	$\hat{U}$	$U = qP$	Factor
217	1	996	1.5	1.21	1.24
217	2	996	.5	1.21	−2.42
219	1	1 830	3.0	2.22	1.35
224	1	4 758	5.0	5.78	−1.16
224	2	4 758	1.0	5.78	−5.78
224	3	4 758	7.0	5.78	1.21
224	4	4 758	5.0	5.78	−1.16
225	1	5 639	2.5	6.85	−2.74
227	1	7 855	9.5	9.54	−1.00
227	2	7 855	19.0	9.54	1.99
227	3	7 855	18.5	9.54	1.94
230	1	11 957	19.0	14.52	1.31
230	2	11 957	15.5	14.52	1.07
230	3	11 957	13.5	14.52	−1.08
232	1	15 279	12.5	18.56	−1.48
234	1	11 893	16.0	14.44	1.11
234	2	11 893	4.0	14.44	−3.61
234	3	11 893	10.0	14.44	−1.44
236	1	14 512	13.5	17.63	−1.31
236	2	14 512	46.0	17.63	2.61
241	1	10 386	31.0	12.61	2.46
241	2	10 386	8.5	12.61	−1.48
243	1	10 811	4.0	13.13	−3.28
243	2	10 811	4.0	13.13	−3.28
243	3	10 811	12.0	13.13	−1.09
246	1	7 462	17.0	9.06	1.88
246	2	7 462	9.5	9.06	1.05
249	1	8 779	20.0	10.66	1.88
249	2	8 779	48.5	10.66	4.55
249	3	8 779	37.5	10.66	3.52
249	4	8 779	15.0	10.66	1.41
249	5	8 779	5.0	10.66	−2.13
253	1	5 187	20.5	6.30	3.25
253	2	5 187	6.0	6.30	−1.05
257	1	6 241	7.5	7.58	−1.01
257	2	6 241	8.0	7.58	1.06

implies the improbable event of very large pools at the beginning and end of the run.

Table 7 shows details of the 1980 reconstructed run for a 10-d pool time. In building the likelihood function (step 2), the following choices have been made: $s_a = 272$, $s_b = 317$, and $N = 17$, so that $\Delta s = 3$ days. Thus, the run is broken into 17 groups of fish, with actual brailer counts in each group shown under the heading "Escapement." The "Catch" column shows how the model apportions catch to each group after solving the backward problem. (Note that this apportionment is more complex than simply adding the daily catch to a single group. For example, see fishery day 238 in Tables 6 and 7.) The "Total" and "Expected" columns correspond to $\hat{A}_j$ and A_j, respectively, in equations (32) and (34). The original brailer record is bimodal, with slightly depressed returns between days 299 and 305. The model fills this depression by adding catch to produce a unimodal total run. The expected run comes from curve (4), which optimally describes the total run.

Table 8 shows the test fishery reconstruction for the 1980 run with a 10-d pool time. This includes the calculated pool size, together with the observed and expected catch per unit effort for each of the 36 sets. Evidently, the observed data are very noisy. Sets on the same day may give widely varying results; however, the model manages to detect the general trend of increase and decline. Multiplicative error factors associated with each set are shown positive when the observation indicates too large a pool and negative otherwise. These are consistent with Table 5 (10-d pool time), which shows a 90% confidence factor of 2.57 and a 95% factor of 4.24. Even though a given test set may lead to a pool estimate out by a factor of 2 or 4, the combined information from several sets over a period appear to give a valid indication of pool size. The in-season use of test data depends primarily on the manager's view of pool time, in conjunction with the schedule of catchabilities in item 6 of the conclusions.

Appendix E gives a brief description of the computer methods involved in working this example. Tables 6–8 give almost a complete 1980 data set for chinook adults. All test sets are reported in Table 8, and the brailer record (magnified to include wild stocks) appears in 3-d groups in Table 7. A partial list of catch data, including all commercial catch, is given in Table 6. Readers interested in a full data set for 1980 and other years should consult Sibert and Schnute (1982). Their report presents further analysis of Alberni Inlet chinook runs, including a description of sex and age structure in the population.

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Appendix A. Notation Summary

This appendix lists all notation in the paper, ordered alphabetically, with the Greek alphabet second. Symbols in the text with the circumflex above refer to observations or estimates of the quantities listed here.

A_j	number of fish in group j ($j = 1, \ldots, N$)
a	run curve parameter proportional to the peak daily run
b	run curve skewness parameter
C, $C(t)$	cumulative catch from all fisheries (at time t)
c, $c(t)$	catch rate from all fisheries, dC/dt
e	exp(1) = 2.71828 . . .; base for natural logarithms
i	index for test fishery sets ($i = 1, \ldots, M$)
j	index for groups of fish ($j = 1, \ldots, N$)
L_1	likelihood function associated with the test fishery
L_2	likelihood function associated with the fishery run curve
ℓ	weighted sum of ℓ_1 and ℓ_2; $\ell = W\ell_1 + \ell_2$
ℓ_1	$-\log(L_1)$, except for a constant independent of parameters
ℓ_2	$-\log(L_2)$, except for a constant independent of parameters
ℓ_{2a}, ℓ_{2b}	components of ℓ_2; $\ell_2 = \ell_{2a} + \ell_{2b}$
M	total number of test fishery sets
N	a number of time intervals in the hatchery; also a corresponding number of groups of fish
P, $P(t)$	number of fish in the fishery pool (at time t)
q	test fishery catchability coefficient
s	time, usually a time in the hatchery; may be used as an integration variable
s_a	time near the beginning of the observed hatchery run
s_b	time near the end of the observed hatchery run
s_f	time after which one observes no further escapement
s_0	typical hatchery arrival day (modeler's choice)
t	time, usually a time in the fishery
t_f	time after which there is no further fishing
t_i	time of test fishery set i ($i = 1, \ldots, M$)
t_0	fishery arrival day corresponding to hatchery s_0
U, $U(t)$	test catch per unit effort (at time t)
u	time, used as an integration variable
W	weight factor giving relative importance of ℓ_1 over ℓ_2
w, $w(s)$	fish per unit time associated with a small group (Appendix A)
X, $X(t)$	cumulative fishery arrivals (at time t)
X_j	cumulative arrivals from groups 1 to j ($j = 1, \ldots, N$)
X_0	0 (arrivals prior to the first group)
X_∞	total run; total fishery arrivals
X^*	$X(\tau^*)$; cumulative fishery arrivals up to the peak day
X'	$X(\tau^*)/X_\infty$; run arrival fraction up to the peak day
x, $x(t)$	fishery arrival rate, dX/dt
x^*	$x(\tau^*)$; peak daily fishery arrivals
x'	$x(\tau^*)/X_\infty$; peak daily arrival fraction in the fishery
Y, $Y(t)$	cumulative fishery escapement (at time t)
y, $y(t)$	fishery escapement rate, dY/dt
Z, $Z(s)$	cumulative hatchery arrivals (at time s)
z, $z(s)$	hatchery arrival rate, dZ/ds
z'	$z(\sigma^*)/X_\infty$; peak hatchery arrival rate fraction (no fishing)
α	run expansion factor (from fishery to hatchery)
β	constant in the linear map between t and s
γ	standard deviation for log normal test fishery errors
Δs	time period in the hatchery used to define N groups
δ	a small time interval (Appendix A)
ϵ_i	predictive error in test fishery set i ($i = 1, \ldots, M$)
σ^*	hatchery peak arrival day (no fishing)
τ	pool time; time spent by fish in the fishery
τ_0	when $0 < b < 1$, the time prior to which $X(t) = 0$
τ^*	fishery peak arrival day
τ_p^*	midpool peak arrival day; $\tau_p^* = \tau^* + \tau/2$

Appendix B. Run Curve Details

Schnute (1981, p. 1132) showed that

(B1) $X^*/X_\infty = (1 - b)^{1/b}$

and

(B2) $x^*/X^* = a/(1 - b)$,

where Schnute's (1981) notation has been converted to the notation used in this paper. Equation (2) is just equation (B1), and equation (3) results from multiplying equation (B1) by equation (B2).

Similarly, Schnute (1981, p. 1132) showed that once $X(t)$ is computed from equation (1), then

(B3) $x = (a/b)\,[(X_\infty/X)^b - 1]X.$

Equation (3) allows a to be eliminated in favor of x', so that equation (B3) can also be written as

(B4) $x = -(1 - b)^{-1/b}(1 - b^{-1})x'\,[(X_\infty/X)^b - 1]X.$

This gives the formula for $x(t)$ when $X(t)$ has been computed from equation (4). A similar equation expresses $z(s)$ in terms of $Z(s)$ from equation (7), namely,

(B5) $z = -(1 - b)^{-1/b}(1 - b^{-1})z'[(X_\infty/Z)^b - 1]Z.$

Equations (1)−(5), (7), and (B3)−(B5) all have limiting forms as the parameter b tends to zero. These are listed in Table B1. From a numerical point of view, the case $b = 0$ is simply a continuous extension of the case $b \neq 0$, provided that formulas in the text are always used in connection with their counterparts in Table B1.

TABLE B1. Counterparts of various text equations when $b = 0$.

Equation No.	Counterpart when $b = 0$
(1), (18)	$X(t) = X_\infty \exp[-e^{-a(t - \tau^*)}]$
(2), (23)	$X' = 1/e$
(3)	$x' = a/e$
(4)	$X(t) = X_\infty \exp[-e^{-ex'(t - \tau^*)}]$
(5)	$t = \tau^* + (ex')^{-1} \log[\log(X_\infty/X)]$
(7)	$Z(s) = X_\infty \exp[-e^{-ez'(s - w^*)}]$
(A3)	$x = a \log(X_\infty/X)X$
(A4)	$x = (x'/e) \log(X_\infty/X)X$
(A5)	$z = (z'/e) \log(X_\infty/Z)Z$

When $b > 0$, there is a time τ_0 for which

(B6) $X(\tau_0) = 0.$

When $X(t)$ is given by equation (4), then equation (B6) becomes an equation that can be solved for τ_0. The result is

(B7) $\tau_0 = \tau^* + x'^{-1}(1 - b)^{(1 - b)/b} \log(b).$

Notice that τ_0 in equation (B7) is defined for $0 < b < 1$. When $b \geq 1$, both equations (4) and (B7) involve undefined quantities, and τ^* in equation (1) no longer corresponds to an inflection point. For further discussion, see the description of the cases $0 < b < 1$ and $b \geq 1$ (regions 1 and 2) in Schnute (1981).

Appendix C. Derivation of Pool Equations (13), (14), and (16).

Let δ represent a small interval of time, and consider the small group of fish that arrive in the fishery between the two times $t - \tau$ and $t - \tau + \delta$. Since $x(t - \tau)$ is the initial rate of arrival, the total number in this group is approximately equal to $x(t - \tau)\delta$. As the group moves through the fishery, it is diminished by the catch. At any later time s, let $w(s)\delta$ represent the number of fish in the group. Between times s and $s + \delta$, the number of fish caught from this group is

(C1) $w(s)\delta - w(s + \delta)\delta = [c(s)\delta][w(s)\delta/P(s)].$

The left side of equation (C1) expresses the catch simply as the net loss to the group. The right side describes the same catch as the product of two factors in square brackets. The first factor is the catch rate $c(s)$ multiplied by the time δ, that is, the total catch from the entire pool between times s and $s + \delta$. The second factor is a fraction representing the proportion of fish in the small group relative to the entire pool. Thus, equation (C1) states that fish are caught from the small group in proportion to the group size relative to the available population.

Divide equation (C1) by δ^2 and take the limit as δ tends to 0. The result is the differential equation

(C2) $dw/ds = cw/P.$

At time $t - \tau$, w equals the arrival rate $x(t - \tau)$, while at the later time t, when fish have been in the pool for a time period τ, w equals the escapement rate $y(t)$:

(C3) $w(t - \tau) = x(t - \tau); \quad w(t) = y(t).$

Equation (13) results from integrating the differential equation (C2) and applying the boundary conditions of equation (C3).

Equation (10) can be written in the form

(C4) $P(t) = \int_{-\infty}^{t} [x(s) - c(s) - y(s)]ds,$

since x, c, and y are just the derivatives of X, C, and Y, respectively. The forward equation (14) follows at once from equations (C4) and (13). Similarly, equation (10) can also be written as

$$\text{(C5)}\quad P(t) = \int_t^\infty [y(s) + c(s) - x(s)]ds,$$

and letting $t = s + \tau$ in equation (13), $x(s)$ can be expressed as

$$\text{(C6)}\quad x(s) = y(s + \tau) \exp\left\{\int_s^{s+\tau} [c(u)/P(u)]du\right\}.$$

The backward equation (16) follows from equations (C5) and (C6). These calculations assume that X, Y, and C are such that the pool begins and ends without fish, that is, that $P(-\infty)$ and $P(\infty)$ are both 0.

Appendix D. Derivation of ℓ_1 and ℓ_2

The negative logarithm of L_1 is

$$\text{(D1)}\quad -\log(L_1) = k + M \log(\gamma) + (\gamma^{-2}/2) \times \sum_{i=1}^{M} [\log(\hat{U}_i/\hat{P}_i) - \log(q)]^2,$$

where k is a constant independent of parameters. The estimates $\hat{q}$ and $\hat{\gamma}$ in equations (38) and (39) result from setting the derivatives of the function in equation (D1) with respect to q and γ both equal to zero. Substituting these estimates into equation (D1) and ignoring k gives ℓ_1 in equation (40).

It follows from equations (31) and (32) that

$$\text{(D2)}\quad \sum_{j=1}^{N} \hat{A}_j = X_\infty.$$

Also, from equation (37)

$$\text{(D3)}\quad -\log(L_2) = -\log(X_\infty!) + \sum_{j=1}^{N} [\hat{A}_j \log(X_\infty) - \hat{A}_j \log(A_j) + \log(A_j!)].$$

By combining equations (D2) and (D3) with (41)−(43), one can show that

$$\text{(D4)}\quad -\log(L_2) = X_\infty \log(X_\infty) - X_\infty - \log(X_\infty!) + \ell_2.$$

Since X_∞ is a known constant in this analysis, equation (D4) justifies the use of ℓ_2 in place of $-\log(L_2)$.

Appendix E. Computer Methods

A program to compute the function ℓ and to solve problem 1, 2, or 3 was first written in Applesoft BASIC to be used on the Apple II microcomputer as a module in Schnute's (1982) implementation of the simplex search method. This worked well, although a little slowly (typical search time of 15−30 min), in finding local minima. It became clear that a full exploration of the contours of ℓ would be needed to find global solutions to problems 1 and 2. This would require a very large number of evaluations of ℓ, a prohibitive task for the Apple II. At this point all programs (including Schnute's implementation of simplex search) were transmitted electronically to the local VAX 11/780 minicomputer and easily converted to VAX BASIC. The module to compute ℓ was used to obtain primitive contour plots of ℓ_1 (problem 1) and ℓ_2 (problem 2) as functions of α, t_0, and τ. These consisted simply of large three-dimensional arrays on a series of pages. The value of pool time τ was fixed on a typical page, so that one could search visually for an optimal pair (α, t_0) corresponding to a given τ. Typical VAX CPU time required to compute one such three-dimensional array (3000 function evaluations) was 5−15 min, depending on the year of data and the function. Minima found by this process were then used, as described earlier, as beginning points in the search for solutions to problem 3.

As a check on this entire process, a separate simulation program was written in VAX FORTRAN to generate artificial data. This program essentially solved the forward problem in simulating the fishery on a run of fish stochastically distributed according to a prescribed run curve. The methods of the previous paragraph led to reasonable estimates of the parameters used in simulation, subject to ambiguities very similar to those detected for real data.

Biochemical Evidence that Winter Flounder (*Pseudopleuronectes americanus*) have Induced Hepatic Cytochrome P-450-Dependent Monooxygenase Activities

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Livers from winter flounder (*Pseudopleuronectes americanus*) captured near Mount Desert Island, Maine, showed marked variation in hepatic benzo[*a*]pyrene hydroxylase (AHH; from 0.04 to 8.8 FU·min^{-1}·mg protein^{-1}) and 7-ethoxyresorufin deethylase activities (7-ERD; from <2 to 1165 pmol·min^{-1}·mg protein^{-1}), and a dichotomy in the effect of 7,8-benzoflavone (ANF) added in vitro on AHH activity. Based on this ANF effect, the flounder could be divided into two groups. One group had high 7-ERD activity and high AHH activity which was inhibited by ANF; the other group had low 7-ERD activity and low AHH activity which was enhanced by ANF. Sex, weight, length, liver weight, gonad weight/body weight ratio, and liver/body weight ratio explained only a small part of the variability in hepatic AHH activities. Electrophoretograms of hepatic microsomes from flounder treated with 1,2,3,4-dibenzanthracene (DBA) or 5,6-benzoflavone (βNF) showed a novel or enriched polypeptide species present near 57 000 daltons, in the molecular weight (MW) range of known cytochrome P-450 isozymes. A polypeptide of similar MW was only faintly discernable in liver microsomes from untreated flounder whose hepatic AHH activity was much lower than that of the treated flounder, whereas a band of this MW was prominent in hepatic microsomes from untreated flounder with high hepatic AHH activity. These results suggest that many of the winter flounder captured near Mount Desert Island, Maine have induced hepatic monooxygenase activity due to exposure to PAH or PAH-like inducers present in their natural habitat.

FOUREMAN, G. L., N. B. WHITE JR., AND J. R. BEND. 1983. Biochemical evidence that winter flounder (*Pseudopleuronectes americanus*) have induced hepatic cytochrome P-450-dependent monooxygenase activities. Can. J. Fish. Aquat. Sci. 40: 854–865.

Les foies de plies rouges (*Pseudopleuronectes americanus*) capturées dans le voisinage de Mt. Desert Island (Maine) montrent une variation marquée des activités de benzo[*a*]pyrène hydroxylase (AHH; de 0,04 à 8,8 FU·min^{-1}·mg protéines^{-1}) et de 7-éthoxyrésorufin dééthylase (7-ERD; de <2 à 1 165 pmol·min^{-1}·mg protéines^{-1}) hépatiques, et une dichotomie de l'effet de 7,8-benzoflavone (ANF) ajouté *in vitro* sur l'activité de AHH. En se fondant sur cet effet de l'ANF, on peut diviser la plie en deux groupes : un groupe a une activité élevée de 7-ERD et une activité élevée de AHH qui est rehaussée par ANF; l'autre groupe a une faible activité de 7-ERD et une faible activité de AHH qui est rehaussée par ANF. Une faible partie seulement de la variabilité des activités de AHH hépatique s'explique par le sexe, le poids, la longueur, le poids du foie, la rapport poids des gonades/poids somatique et le rapport foie/poids somatique. Des électrophorétogrammes de microsomes hépatiques de plies traitées à 1,2,3,4-dibenzanthracène (DBA) ou à 5,6-benzoflavone (βNF) révèlent la présence d'une espèce nouvelle ou enrichie de polypeptide présente à proximité de 57 000 daltons, dans la gamme des poids moléculaires (MW) d'isozymes connus du

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cytochrome P-450. On ne peut discerner que faiblement un polypeptide de poids moléculaire semblable dans les microsomes hépatiques de plies non traitées dont l'activité de AHH hépatique est de beaucoup inférieure à celle de plies traitées, alors qu'une bande de même poids moléculaire est proéminente dans les microsomes hépatiques de plies non traitées et à grande activité de AHH hépatique. Ces résultats donnent à penser qu'un grand nombre de plies capturées près de Mt. Desert Island (Maine) ont une activité de monooxygénase hépatique provoquée par exposition à PAH ou à des inducteurs ressemblant à PAH présents dans leur habitat naturel.

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CHARACTERIZATION of the hepatic and extrahepatic monooxygenase systems of fish has so far demonstrated many similarities with the well-characterized mammalian systems, including the presence of cytochrome P-450. In several teleosts, electron spin resonance signals from cytochrome P-450 in liver microsomes were very similar to those found in mammals (Chevion et al. 1977; Stegeman and Chevion 1980). Also, the mechanism of transferring reducing equivalents to cytochrome P-450 appears to be very similar to that of mammals, the ratio of the flavin moieties in NADPH-cytochrome P-450 reductase in little skate (*Raja erinacea*) being the same as in rabbit (Serabjit-Singh et al. 1981). To date, the number and structure of compounds which have been demonstrated as substrates for aquatic cytochrome P-450-dependent monooxygenase systems are as varied as they are for mammalian systems (for review see Bend and James 1978). Although exceptions do occur (Ahokas et al. 1977; Pederson et al. 1976), the specific activities of hepatic microsomes from fish measured under optimal conditions for a given substrate are, in general, markedly lower than for laboratory mammals.

Induction of the cytochrome P-450-dependent monooxygenase system is well documented in mammalian species and occurs in response to treatment with two major types of compounds. One is typified by phenobarbital (PB) and other barbiturates and the other is typified by 3-methylcholanthrene (3-MC) and other polycyclic aromatic hydrocarbons (PAH), certain PCB, PBB and chlorinated dioxin isomers, and some flavonoids, such as βNF (Conney 1967). Induction by the PAH-class of compounds usually results in the formation of a novel form or forms of cytochrome P-450 (e.g. cytochrome $P\text{-}450_1$) and elevation in enzyme rates such as 7-ethoxyresorufin deethylase (7-ERD) activity and benzo[*a*]pyrene hydroxylase (AHH) activity. Additionally, it is known that 7,8-benzoflavone (ANF) inhibits this latter activity in hepatic microsomes from rats or skates treated with PAH but either does not affect or, in some cases, enhances AHH activity in hepatic microsomes from control rats and skates (Wiebel et al. 1971; Bend et al. 1977).

Many inducers of the PAH-type are thoroughly documented as terrestrial and aquatic pollutants (Stegeman 1981) and several studies have suggested a correlation between levels of hepatic AHH activity in fish and areas with high levels of PAH and PAH-type contaminants (Payne 1976; Dunn 1980). Such results indicate that environmental induction may occur and that it may be possible to distinguish animals that have been exposed to inducing compounds. The study reported here arose from the large variations in hepatic AHH activities we noted in a population of winter flounder (*Pseudopleuronectes americanus*), a marine teleost.

The goals of this investigation are to characterize the variation in monooxygenase activity and to compare biochemical properties of the cytochrome P-450-dependent monooxygenase system in the untreated flounder population to those in flounder treated with PAH-type enzyme inducers.

Materials and Methods

FISH CAPTURE, TREATMENT, AND TISSUE PREPARATION

Winter flounder (*Pseudopleuronectes americanus*) were caught by dragnet from the same area (about 6.5 km seaward of Sand Beach on the southeast side of Mt. Desert Island, Maine) and transferred to a 4000-L tank equipped with flowing seawater (12–15°C). No bacteriostats or fungistats were used in the tank or water system. After a minimum acclimitization period of 2-d post capture, the fish were sacrificed by decapitation. A few flounder were kept for up to 2 wk and showed no adverse effects. Livers (with gallbladders resected) or kidneys were removed immediately and placed on ice in 1.15% KCl, 1.25 mmol/L *N*-2-hydroxyethylpiperazine-N′-2-ethanesulfonic acid (HEPES), pH 7.5 (solution A). In some flounder, that portion of gut from just distal to the pyloric sphincter to proximal to the anal sphincter was removed and washed in at least 20 mL of solution A. The guts were then cut open lengthwise and the mucosa scraped from the gut wall. The tissues (liver, kidney, or gut mucosa) were blotted, weighed, and homogenized in solution A with a Potter–Elvejehm homogenizer. Four passes of a motor-driven teflon pestle were used for each tissue. Kidneys were homogenized in 2 mL total volume, while liver and gut homogenates were 15 and 25% wt/vol, respectively.

Microsomes were prepared by first centrifuging the tissue homogenate at 13 000 *g* for 20 min to remove cell debris, nucleii, and mitochondria. The resultant supernatant was ultracentrifuged at 176 000 *g* for 45 min; the microsomal pellet was resuspended by hand in solution A and then centrifuged again at 176 000 *g* for 30 additional min. All steps were performed at 0–4°C. Clear portions were withdrawn from the microsomal supernatant fraction (cytosol) and used for the assay of cytosolic enzyme activities.

Winter flounder were also captured by dragnet in April and May of 1980, near the mouth of the West Passage of Narragansett Bay, about 19 km from Newport, Rhode Island.

The fish were double-bagged in pinch-sealed plastic bags with 250–300 mL of oxygenated seawater, placed in large polystyrene containers (Fisher No. 11-676-18) with abundant quantities of ice and shipped by air to our North Carolina lab. Even after 10 h under these conditions, all fish were active and appeared healthy. These flounder were maintained in our lab in 1000-L aquaria (Instant Ocean Culture System, CS-250) at 15°C and 850 mOsmol/L of ocean salts (Instant Ocean Mix, Eastlake, Ohio). Fish were killed and assays conducted within 48 h of arrival.

Treatment of fish with PAH-type inducing agents was by intraperitoneal (IP) injection of a single dose (100 mg/kg) of βNF in corn oil (13 mg/L) or three doses (10 mg/kg each) of DBA in corn oil (8 mg/mL) injected on consecutive days. The animals were sacrificed on the 10th day after the initial injection.

Enzyme Assays and Electrophoresis

AHH activity was assayed essentially according to Wattenberg et al. (1962). A NADPH regenerating system was employed which contained 5 mmol/L of both glucose-6-phosphate (disodium salt) and $MgSO_4$, 0.5 mmol/L NADP and 2 units (Sigma) of glucose-6-phosphate dehydrogenase. The incubation mixture was buffered at pH 7.6, with 0.1 mol/L HEPES, contained 4 mg bovine serum albumin, between 2 and 4 mg of homogenate or microsomal protein and had a final volume of 2.5 mL. Incubation (usually 20 min) was started by addition of benzo[*a*]pyrene (0.63 mmol/L final concentration added in 0.05 mL acetone) and was at 30°C. The reaction was stopped by the addition of 1 mL ice-cold acetone. Blanks were incubated under identical conditions except that the substrate was added immediately after the addition of the acetone. Heptane (7 mL) was then added to the incubation mixture after which it was sealed, vortexed and allowed to sit overnight in the dark at 4°C. The following day, under subdued light, 2.5 mL of 1 mol/L NaOH were added to a 2.5-mL aliquot of the heptane extract of each sample; the mixture was vortexed, centrifuged and the fluorescence of the aqueous layer read on a Turner 430 fluorimeter at excitation 400 nm and emission 525 nm. Results are expressed in relative fluorescence units (FU) where 1 FU equals the fluorescence of a 3 μg/mL quinine sulfate·2 H_2O solution in 0.05 mol/L sulfuric acid at these same wavelengths, and is equivalent in fluorescence to 3.87 nmol 3-hydroxybenzo[*a*]pyrene/mL in 1 mol/L NaOH. (For comparative purposes, AHH activities obtained under these conditions in rat whole liver homogenates were 3.0 ± 0.3 FU·min^{-1}·mg homogenate protein^{-1}). ANF or metyrapone was added to some incubation mixtures (0.5 mmol/L in 0.05 mL acetone) immediately prior to the addition of the substrate. Based on 3 mg of homogenate protein in an incubation mixture, the minimum detectable AHH activity was 0.01 FU·min^{-1}·mg protein^{-1}.

A fluorimetric method (Burke and Mayer 1974) was employed for the assay of 7-ERD activity at a temperature of 30°C, at substrate and NADPH concentrations of 2 and 20 μmol/L, respectively, at a final pH of 7.8, and a buffer (HEPES) concentration of 0.1 mol/L. The incubation mixture was internally standardized with resorufin (Pierce Chemical Co., Rockford, Illinois), the product of the reaction. The minimum detectable level of activity with this assay was 2 pmol of resorufin formed·min^{-1}·mg^{-1} protein.

Glutathione transferase activity (GST) was measured using 2,4-dinitrochlorobenzene (DNCB) as substrate (1.0 mmol/L added in 0.01 mL dimethyl sulfoxide) with glutathione (5.0 mmol/L) as cosubstrate with 0.1 mol/L phosphate buffer, pH 6.6, all in a volume of 3 mL (Booth et al. 1961). Product formation was followed at 340 nm in a Gilford 300-N spectrophotometer at 30°C. Cytosolic fractions were used as the enzyme source. The molar extinction coefficient used for the product of the reaction was 9600 L·mol^{-1}·cm^{-1}.

UDP-Glucuronosyltransferase activity was determined fluorimetrically according to Aitio (1974) using 4-methylumbelliferone as the aglycone substrate. Boiled microsomes were used for enzyme blanks.

A method based on that reported by Cochin and Axelrod (1959) was used to quantify formaldehyde released during benzphetamine *N*-demethylation. A NADPH regenerating system was used as described above for the assay of AHH activity. Parallel incubation mixtures, to which substrate was added after addition of $ZnSO_4$, were used as reaction blanks. Benzphetamine *N*-demethylase activities are reported as nmol HCHO formed·min^{-1}·mg^{-1} protein.

The cytochrome P-450 content of microsomes was quantitated by the dithionite difference procedure with a Beckman DW-2 spectrophotometer in the split beam mode (Omura and Sato 1964).

The Lowry method was used for the estimation of protein content of various subcellular fractions, bovine serum albumin serving as the standard (Lowry et al. 1951).

Sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) was performed according to Laemmli and Favre (1973) using 7.5% polyacrylamide slab gels with a 3% stacking gel. Standards used and their molecular weights were BSA (68 000), ovalbumin (45 000), and carbonic anhydrase (32 000). Protein bands were stained in 0.115% Coomassie Brilliant Blue (R-250) for at least 45 min prior to washing away unfixed stain in several changes of 25% ethanol/8% acetic acid. Samples (2–3 mg of microsomal protein) were treated for 2 min at 90°C in a solution containing 10% glycerol, 3% SDS, and 5% 2-mercaptoethanol with 0.004% bromphenol blue as the tracking dye.

Results

Variation of in vitro Hepatic Monooxygenase Activity of Maine Winter Flounder

Initially, two cytochrome P-450-dependent monooxygenase activities were measured in both liver homogenate and hepatic microsomes in winter flounder caught near Mt. Desert Island, Maine. These included 7-ERD activity and AHH activity, in addition to the response of AHH activity to ANF added in vitro. An obvious characteristic of these data (Table 1) was the variation in enzyme activities encountered. AHH activities of liver microsomes varied over 40-fold while 7-ERD values ranged almost 500-fold. A differential response to in vitro ANF (0.5 mmol/L) was also observed. In fish having relatively low hepatic AHH activity (Nos. 1 and 2),

TABLE 1. Comparison of hepatic benzo[*a*]pyrene hydroxylase (AHH) activity (in the presence and absence of 0.5 mmol/L 7,8-benzoflavone [ANF]) and 7-ethoxyresorufin deethylase (7-ERD) activity in whole homogenate and washed microsomes from individual winter flounder.[a]

Fish no.	Enzyme source	AHH activity (FU·min^{-1}·mg protein^{-1}) Without ANF	AHH activity (FU·min^{-1}·mg protein^{-1}) With ANF	7-ERD activity (pmol·min^{-1}·mg protein^{-1})
1	Homogenate	0.17	0.72	<2[b]
	Microsomes	0.55	3.36	<2
2	Homogenate	0.60	0.78	26
	Microsomes	1.65	3.21	175
3	Homogenate	1.12	0.79	67
	Microsomes	2.86	2.38	219
4	Homogenate	1.47	1.09	75
	Microsomes	3.06	2.72	305
5	Homogenate	1.73	0.98	130
	Microsomes	4.51	3.40	450
6	Homogenate	2.21	0.96	67
	Microsomes	8.36	3.57	219
7	Homogenate	2.97	1.04	116
	Microsomes	9.59	2.91	610
8	Homogenate	7.36	2.49	617
	Microsomes	23.10	5.84	947

[a]Results presented are from fish all killed and assayed on the same day.
[b]Sensitivity of assay procedure.

TABLE 2. Relationship by year of hepatic AHH activities, hepatic 7-ERD activities and percent of fish with hepatic AHH activity inhibited by ANF in winter flounder.

Year[a]	*n*	$\bar{x}$ AHH ± SD (Range)	$\bar{x}$ 7-ERD ± SD (Range)	% Fish with AHH activity inhibited by ANF
78	172	1.8±1.7 (0.04–8.8)	131±128 (<2–837)	49[c]
79	81	2.0±1.9 (0.10–8.0)	114±143 (<2–796)[b]	72
80	86	1.8±1.6 (0.08–6.1)	237±216 (<2–1165)[b]	84[c]
81	74	1.3±1.2 (0.06–6.4)	62±55 (<2–196)	68

[a]June–August.
[b]Different from the following season ($P < 0.05$), Duncan Multiple Range Test.
[c]Different from the following season ($P < 0.02$), chi-square analysis.

addition of ANF enhanced AHH activity whereas in fish with higher hepatic AHH activities, ANF acted as an inhibitor (No. 8). It should also be noted that AHH and 7-ERD activities parallel one another. In all instances, the responses of AHH activity to ANF and the relative levels of 7-ERD and AHH activities measured in microsomes were reflected in assays on the respective homogenates. This fact enabled us to determine these enzyme activities using whole homogenate of liver.

RECURRENCE OF VARIATION IN SELECTED MONOOXYGENASE ACTIVITIES IN LIVER OF WINTER FLOUNDER

Table 2 gives the statistical analysis of hepatic AHH activities, hepatic 7-ERD activities and the percent of fish with hepatic AHH activity which was inhibited by ANF by year from 1978 to 1981. The mean AHH activity of any given year was not different from that of the following year (all analyses were performed between June and August). However, the mean hepatic AHH values between 1979 and 1981 were different. Similar analyses performed on 7-ERD activities showed that significant differences existed between 1979 and 1980, and 1980 and 1981. There was also considerable variation in the percentage of flounder sampled that had hepatic AHH which was inhibited by ANF. This variation is also demonstrated graphically by the frequency distribution of hepatic AHH activities for each year, shown in Fig. 1. The arrow on the abscissa of each plot indicates that value of hepatic AHH activity which was unchanged by ANF addition. The livers of those fish to the right of the arrows had AHH activities which were enhanced by ANF while those to the left of the arrows had AHH activities which were inhibited by ANF. The mode of hepatic AHH activity was the same for the first 3 yr (AHH activities from 0.5 to 1.0 FU·min^{-1}·mg protein^{-1}), but shifted downward for the 1981 season.

The variable DIFF represents that portion of hepatic AHH activity which was inhibited by 0.5 mmol/L ANF and was obtained by subtracting the AHH activity recorded in the presence of ANF from the AHH activity determined in the absence of ANF. The correlation coefficient (r) obtained from simple regression analysis of DIFF with 7-ERD activity was 0.69 ($n = 388$; $P < 0.001$).

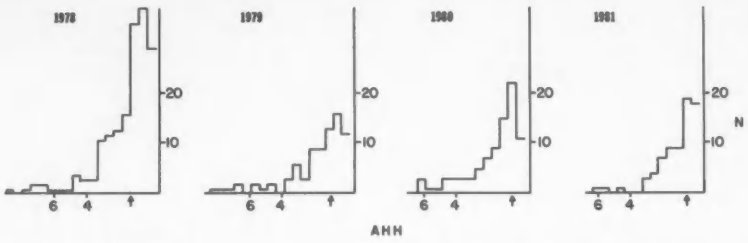

FIG. 1. Frequency distribution of hepatic AHH activities in winter flounder (*Pseudopleuronectes americanus*) homogenates examined, 1978 through 1981. That portion of each year's population to the left of the arrow had AHH activities which were inhibited by 0.5 mmol/L 7,8-benzoflavone (ANF) while that portion to the right had AHH activities which were enhanced by this same concentration of ANF. Total N of each year was 172, 81, 86, and 71 for 1978–81, respectively. AHH activity is expressed in FU·min^{-1}·mg homogenate protein^{-1}.

TABLE 3. Cytochrome P-450 content and AHH activity of hepatic microsomes from winter flounder.

Fish no.	Cytochrome P-450 (nmol/mg protein)	λMax (nm)	AHH (FU·nmol P-450^{-1}·min^{-1})
1	0.60	448.4	6.4[a]
2	0.25	451.0	0.7[b]
3	0.23	450.4	1.1[a]
4	0.18	450.2	3.1[a]
5	0.16	450.8	1.1[a]
6	0.12	450.2	1.8[a]
7	0.12	450.0	0.9[a]

[a]AHH activity inhibited by in vitro addition of 0.5 mmol/L 7,8-benzoflavone (ANF).
[b]AHH activity increased by in vitro addition of 0.5 mmol/L ANF.

COMPARISON OF HEPATIC BENZPHETAMINE *N*-DEMETHYLASE (BND) ACTIVITY AND CYTOCHROME P-450 CONTENT WITH HEPATIC AHH ACTIVITY IN WINTER FLOUNDER

AHH activity and BND activity, another cytochrome P-450-dependent monooxygenase, were measured in liver homogenates from several winter flounder, and plotted as a function of one another. The overall range of AHH activities in these fish was wide, almost 25-fold (from 0.3 to 7.28 FU·min^{-1}·mg protein^{-1}), while the range of their BND activities was just slightly more than 2-fold (0.36–0.78 nmol of HCHO formed·min^{-1}·mg protein^{-1}).

The cytochrome P-450 content, the wavelength of maximum absorption and the AHH activity normalized for cytochrome P-450 content in hepatic microsomes of several winter flounder is given in Table 3. The cytochrome P-450 spectrum of hepatic microsomes from the fish with the highest AHH activity and the highest microsomal cytochrome P-450 content was shifted towards 448 nm indicative of large amounts of cytochrome P-448 in these microsomes as in rat liver after induction with PAH. However, there was no pattern discernable in the shift of the wavelength maxima relative to the hepatic AHH activity in the other flounder livers. The total amount of cytochrome P-450 present/mg microsomal protein and the AHH activity of the same microsomes showed no obvious relationship.

TREATMENT OF FLOUNDER WITH PAH-TYPE INDUCERS AND COMPARISON TO UNTREATED FLOUNDER

After treatment of flounder with either DBA or βNF (see "Materials and Methods"), we observed that all fish had high hepatic 7-ERD activities and high hepatic AHH activities (Table 4). In the eight flounder so treated, the hepatic AHH activity was inhibited by 0.5 mmol/L ANF.

Microsomes were prepared from winter flounder treated with DBA or βNF as well as from other untreated fish and all microsomes were compared by electrophoresis on SDS-PAGE. Figure 2 shows an electrophoretic pattern obtained with hepatic microsomes from 2 untreated flounder, a flounder treated with βNF and a flounder treated with DBA. An intensely staining band, of approximate MW 57 000, was observed in the microsomes from the flounder treated with DBA and βNF (Nos. 3 and 4). A faint band(s) of the same MW was seen in both of the untreated flounder (Nos. 1 and 2). The presence and staining intensity of the band correlates approximately with the AHH activity of the liver homogenates from these fish, which was 1.6, 0.7, 13.0, and 10.6 FU·min^{-1}·mg protein^{-1} for Nos. 1–4, respectively. Thus, the electrophoretic band was present, but faint, in the untreated flounder with low hepatic AHH activities and was a major band in the flounder treated with βNF or DBA, whose AHH activities were high. 7-ERD activities also paralleled

TABLE 4. Hepatic benzo[*a*]pyrene hydroxylase (AHH) and 7-ethoxyresorufin deethylase (7-ERD) activities in liver homogenate of DBA and βNF-treated winter flounder.

Treatment[a]	AHH		7-ERD
	Without ANF	With ANF	
DBA	10.6[b]	1.6	1147[c]
DBA	7.7	1.5	630
DBA	4.0	1.3	1608
βNF	13.0	3.0	1787
βNF	5.8	1.3	1066
βNF	3.0	0.8	795
βNF	3.8	1.2	1259
βNF	3.9	0.9	1431

[a]Either 10 mg/kg of 1,2,3,4-dibenzanthracene (DBA) IP for 3 d or a single IP injection of 5,6-benzoflavone (βNF) at 100 mg/kg. See "Materials and Methods" for details.

[b]Activity is expressed as FU·min^{-1}·mg homogenate protein^{-1}. Incubates were performed in 2 sets: 1 set with 0.5 mmol/L 7,8-benzoflavone (ANF; in acetone), the other with just acetone.

[c]Activity is expressed in pmol resorufin formed·min^{-1}·mg homogenate protein^{-1}.

this trend. This relationship is also demonstrated by the data in Fig. 3. A polypeptide of MW 57 000 was obvious in hepatic microsomes from an untreated flounder having high AHH activity (6.1 FU·min^{-1}·mg homogenate protein^{-1}, channel 1) and was not discernable in hepatic microsomes from an untreated flounder with very low AHH activity (0.1 FU·min^{-1}·mg homogenate protein^{-1}, channels 2 and 3).

Specificity of Enzyme Induction in Flounder Liver

Glutathione transferase (GST) and UDP-glucuronosyltransferase (GT) activities, hepatic enzymes that are also known to be induced by administration of PAH-type compounds to mammals, were determined in liver of untreated, DBA-treated and βNF-treated flounder and are presented in Table 5. The range of hepatic AHH activities in each group of flounder examined is also shown. GT activities of βNF-treated flounder were significantly higher than activities obtained for untreated flounder but GT activities of the DBA-treated flounder were not different from untreated values. Specific GST activity appeared not to be affected by either treatment. The observation that the range of hepatic AHH activities in these untreated flounder was about 60-fold while GT and GST activities of these same fish both varied less than 3-fold, was also of interest.

Extrahepatic AHH Activities

The AHH activity of kidney and gut, two extrahepatic tissues involved in the clearance of xenobiotics, was examined in both untreated and PAH-treated flounder (Table 6). Analysis of gut AHH activity in a total of 48 untreated flounder showed that there was no relationship to hepatic AHH activities ($r = 0.05$; $n = 48$). Where gut AHH activity could be quantitated in either control or PAH-treated fish, it was always enhanced by the addition of ANF. Also, no 7-ERD activity was found in gut tissue of any untreated or PAH-treated flounder tested.

Renal AHH activity of flounder was low and was enhanced by ANF in 30 of the 31 fish examined despite the fact that hepatic AHH activity was high and inhibited by ANF in 85% of these same fish. This was also the case in the flounder treated with DBA, which showed induced hepatic AHH activities. However, renal AHH activities of the flounder treated with βNF were higher than renal AHH activities in DBA-treated or untreated fish and these activities were inhibited by ANF.

Variation of Hepatic AHH and 7-ERD Activities in Winter Flounder from Rhode Island

Hepatic 7-ERD activities and AHH activities (with and without ANF) of several winter flounder caught in Narragansett Bay, RI, were measured for comparison to the Maine data. Although the upper limit of AHH activity was lower in this population than in those near Mt. Desert Island (1.93 vs. 8.8 FU·min^{-1}·mg protein^{-1}), there was a reasonable correlation between 7-ERD and AHH activities ($r = 0.77$; $n = 13$) and the DIFF and 7-ERD activity ($r = 0.79$; $n = 13$). The Rhode Island flounder also demonstrated the dichotomous response to in vitro ANF; 92% (12 of 13) of the fish examined had hepatic AHH activities which were inhibited by ANF while the AHH activity of one flounder was enhanced by ANF and had undetectable 7-ERD activity.

Relationships Between Physical Characteristics of Winter Flounder and Heterogeneity of Hepatic AHH Activity

Several physical characteristics of the sampled fish were tested for correlation with hepatic AHH activity. Weight and length, indices of age, were both tested. Liver weight and liver weight/body weight ratios were also examined as were gonad weight, gonad weight/body weight ratios, feeding status (particulate matter present in or absent from the gut), sex, month (June to August) and year of assay were also tested. Simple regression analysis of these variables with hepatic AHH activity is presented in Table 7. Absolute correlations (r) for these variables ranged from 0.08 ($n = 410$) with the year to 0.29 ($n = 410$) in the case of both liver weight and liver weight/body weight ratio. Also, it should be noted that the characteristics with the highest correlation coefficients (liver wt or liver wt/body wt ratio) could explain only 8.4% of the variability observed in hepatic AHH activity ($r^2 = 0.084$). Although these correlations are all quite low, six of the ten listed were statistically significant ($P < 0.05$). However, when simple linear regression analysis was performed with hepatic AHH activity and 7-ERD activity alone and multiple regression analysis then performed with AHH activity and 7-ERD activity plus these six variables, the r^2 increased only from 0.49 to 0.53. In other words, the inclusion of all the statistically significant parameters from Table 7 was able to explain only 4% more of the variability of hepatic AHH activity than could 7-ERD activity by itself.

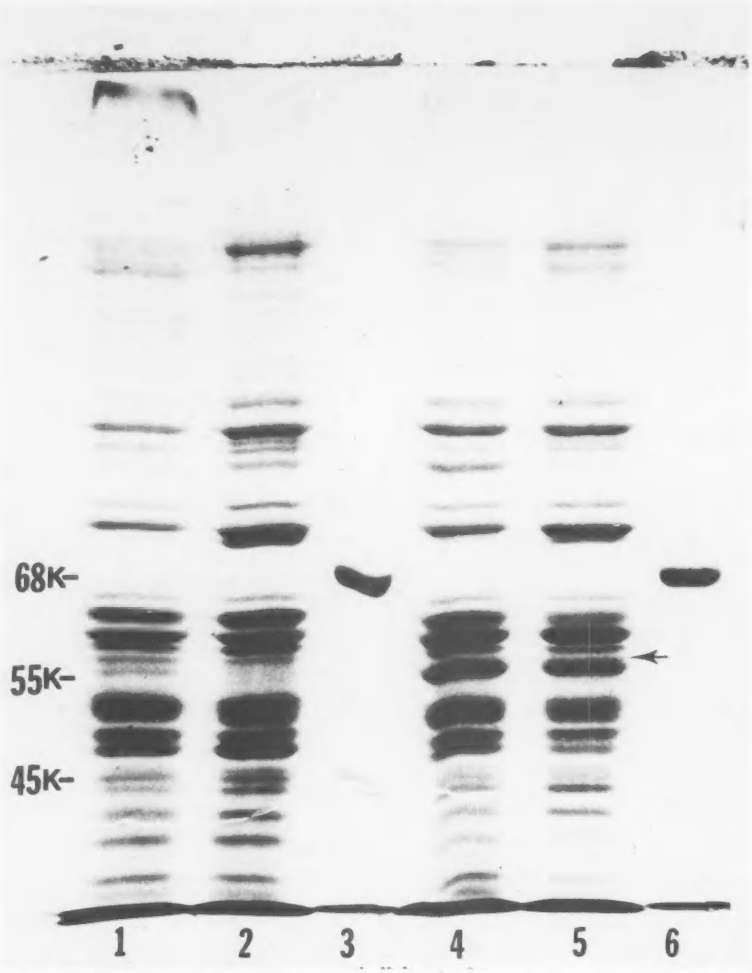

FIG. 2. SDS-Polyacrylamide gel electrophoresis of hepatic microsomes from untreated, DBA-treated[a], and βNF-treated[b] winter flounder. Standards are 5 μg each of BSA (MW 68 000) and ovalbumin (MW 45 000). The arrow indicates the area of 57 000 MW. 0.225 mg of microsomal protein was applied to each channel. AHH and 7-ERD activities of hepatic homogenates and whether the microsomes are from treated or untreated flounder are as follows:

Channel	Fish Status	AHH	7-ERD
1	untreated	1.6[c]	170[d]
2	untreated	0.7	106
4	treated (βNF)	13.0	1787
5	treated (DBA)	10.6	1147
3, 6	standards		

[a]Ten mg/kg of 1,2,3,4-dibenzanthracene thrice, 24 h apart; see text for details.
[b]One-hundred mg/kg of 5,6-benzoflavone; see text for details.
[c]Activity is expressed in FU·min^{-1}·mg homogenate protein^{-1}.
[d]Activity is expressed in pmol resorufin formed·min^{-1}·mg homogenate protein^{-1}.

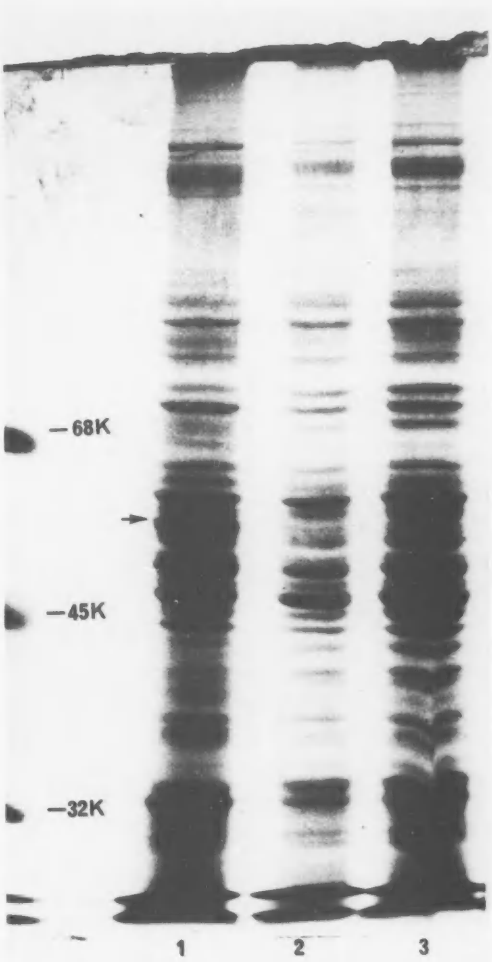

FIG. 3. SDS-Polyacrylamide gel electrophoresis of hepatic microsomes from 2 wild winter flounder with widely different hepatic AHH activities; 6.1 FU·min^{-1}·mg homogenate protein^{-1} in channel 1 and 0.1 FU·min^{-1}·mg homogenate protein^{-1} in channels 2 and 3; 0.15 mg of protein was applied to channels 1 and 3, 0.075 mg to channel 2. Standards (5 μg each) applied to other channels; MWs were BSA, 65K; ovalbumin, 45K; carbonic anhydrase, 32K.

Discussion

The variation observed in the hepatic cytochrome P-450-dependent 7-ERD and AHH activities of winter flounder caught near Mt. Desert Island are marked (over 500-fold in the case of 7-ERD) and recurrent. The year-to-year uniformity of the mean values, ranges (Table 2) and most notably, the frequency distribution of AHH activities in the sampled populations (Fig. 1), establish that this variation is a persistent feature of the flounder population around Mt. Desert Island. It is an important point that without a relatively large sample size, this uniformity in AHH activity distribution may have been obscured. Such observations also emphasize the importance of studying enough fish to conduct statistical analysis of data from wild populations to establish relationships between AHH activities or other endpoints and possible effectors. This large variation in cytochrome P-450-dependent monooxygenase activity is substrate specific for compounds [7-ethoxyresorufin and benzo[*a*]pyrene] whose rate of metabolism is dramatically increased in mammalian and fish hepatic microsomes following exposure of the animal to PAH or PAH-type compounds (James and Bend 1980). Thus, the livers of some of these winter flounder have a biochemical characteristic of PAH-induced monooxygenase systems.

The DIFF represents that portion of hepatic AHH activity in each fish which is affected by ANF. The validation of ANF as an in vitro probe which selectively inhibits metabolism by cytochrome P-450 forms which are induced by compounds of the PAH class is supported by a growing body of experimental evidence (Goujon et al. 1972; Jellinck et al. 1975; Bend et al. 1977; Huang et al. 1981). That ANF worked similarly in these fish is supported by data in Table 4 where the hepatic AHH activity of all fish treated with DBA or βNF was inhibited by ANF. It is likely then that when positive, DIFF represents that portion of hepatic AHH activity due to cytochrome species with PAH-induced characteristics. This inhibition of AHH by ANF is consistent with the existence of one or more forms of cytochrome P-450, with PAH-induced characteristics, in the livers of many of these flounder.

The wide and significant annual variation (Table 2) of 7-ERD activities and the nonparallel nature of these fluctuations with hepatic AHH activity indicate that these two activities are not closely associated. Such results are most easily explained by assuming the presence of multiple forms of cytochrome P-450 in the livers of these flounder. This is certainly known to be the case in mammalian species and at least one fish species treated with PAH-type compounds (Haugen et al. 1976; Negishi and Nebert 1979; Stegeman et al. 1981).

In many mammalian species, the response of liver to the administration of PAH-like inducers is manifested by dramatic increases in AHH activity, and a hypsochromic shift in the wavelength of maximal absorption of the cytochrome(s) P-450 in its CO-ligated and reduced form, from 450 to 448 nm. However, in the winter flounder examined (Table 3), there was no clear relationship between AHH activity and hepatic cytochrome P-450 content or a hypsochromic spectral shift. Similar circumstances have been observed by other workers in little skates (Bend et al. 1977) and in trout (Pederson et al. 1976) treated with PAH. In little skates, subsequent analysis of the cytochrome P-450 of hepatic microsomes from PAH-induced fish demonstrated the presence of a cytochrome P-448 species which was absent in untreated animals (Bend et al. 1979). However, cytochrome P-448 was not the major form of cytochrome present in the treated skates, its amount/characteristics being inadequate in nature to cause a shift in the observed spectra of hepatic microsomes. A similar situation in these fish probably

TABLE 5. UDP-Glucuronosyltransferase, glutathione transferase, and the range of AHH activities in hepatic tissue of DBA-treated[a], βNF-treated[b] and wild winter flounder.

Treatment (*n*)	Hepatic AHH (Range)	UDP-Glucuronosyltransferase	Glutathione Transferase
Wild (10)	0.1–6.0	6.5±1.8	—
DBA (3)	4.0–10.6[c]	9.5[d]±4.5 (N.S.)	1.50[e], 1.45 (N.S.)
βNF (5)	3.0–13.0	12.3[f]±4.2 ($P < 0.01$)	1.65±0.6
Wild (34)	0.5–6.1	—	1.69±0.8

[a]Ten mg/kg of 1,2,3,4-dibenzanthracene (DBA) was injected IP in corn oil for three successive days, 24 h apart. Sacrifice was on the 10th day after the first injection.

[b]One hundred mg/kg of 5,6-benzoflavone (βNF) was injected IP in corn oil. Sacrifice was on the 10th day after injection.

[c]AHH is expressed as FU·min^{-1}·mg homogenate protein^{-1}.

[d]Activities in pmol 4-methylumbelliferone conjugated·min^{-1}·mg microsomal protein^{-1}.

[e]Activities are expressed in μmol of 2,4-dinitrochlorobenzene conjugated with GSH·min^{-1}·mg cytosolic protein^{-1}.

[f]Mann–Whitney *U*-Test.

TABLE 6. Benzo[*a*]pyrene hydroxylase (AHH) in homogenate of DBA-treated[a], βNF-treated[b], and wild winter flounder: Hepatic, intestinal, and renal activities and the effect of 7,8-benzoflavone (ANF) on these activities.

Fish no.	Treatment	Hepatic AHH		Intestinal AHH		Renal AHH	
		w/o ANF	w/ANF	w/o ANF	w/ANF	w/o ANF	w/ANF
90	Wild	6.02[c]	1.8	<0.01	<0.01	—[d]	—
74	Wild	4.5	2.7	0.17	1.29	—	—
61	Wild	0.7	0.3	0.01	0.02	—	—
82	Wild	0.1	0.3	0.01	0.01	—	—
7	DBA	10.6	1.6	<0.01	<0.01	<0.01	0.05
10	DBA	7.7	1.5	0.26	1.14	0.04	0.04
1	DBA	4.0	1.3	<0.01	0.03	0.04	0.12
2	βNF	13.0	3.0	0.20	0.75	—	—
5	βNF	5.8	1.3	0.41	1.52	—	—
8	βNF	3.0	0.8	0.05	0.39	0.18	0.08
9	βNF	3.8	1.2	0.05	0.15	0.09	0.04
12	βNF	3.9	0.9	0.02	0.09	0.58	0.15

[a]Ten mg/kg 1,2,3,4-dibenzanthracene, IP; see text for specifics.

[b]One-hundred mg/kg 5,6-benzoflavone, IP; see text for specifics.

[c]Activity is expressed in FU·min^{-1}·mg protein^{-1}. Two sets of incubation mixtures were run with each tissue; one containing 0.5 mmol/L 7,8-benzoflavone (ANF, in acetone) and the other containing just acetone.

[d]Dashes indicate values which were not determined.

TABLE 7. Correlation coefficients (*r*) of several physical characteristics with hepatic AHH activity of winter flounder.

Parameter	*r*	*n*	*P*
Liver weight	−0.29	410	<0.001
Liver wt/body wt	−0.29	410	<0.001
Weight	−0.24	410	<0.001
Sex[a]	+0.19	410	<0.001
Month of assay	−0.19	410	<0.001
Length	−0.18	345	<0.001
Feeding status[b]	−0.15	153	0.051
Gonad wt	−0.14	174	0.066
Gonad wt/body wt	+0.12	174	0.066
Year of assay	−0.08	410	0.081

[a]Indicates males had higher hepatic AHH activities.

[b]Indicates that fish without particulate matter in the gut had higher hepatic AHH activities.

accounts for much of the data in Table 3. In addition, these data also indicate heterogeneity of the cytochrome P-450 species present in the liver tissues of these fish as the AHH activities/nmol cytochrome P-450 were not at all uniform. Thus, neither a hypsochromic shift in the hepatic microsomal P-450 spectrum nor the microsomal cytochrome P-450 content are reliable indicators of PAH-type monooxygenase induction in this species.

That the elevated AHH and 7-ERD activities observed in many of these winter flounder are due to exposure to PAH or PAH-like compounds is strongly supported by the enzymatic data in Table 4 and the electrophoretic data in Fig. 2 and 3. The hepatic AHH activities of all flounder treated with either DBA or βNF were elevated, and were inhibited by ANF; in untreated flounder, ANF inhibited all hepatic AHH activities which were greater than 1.6 FU·min^{-1}·mg protein^{-1} (i.e. 262 of 410 flounder; Table 2). Such results are most

readily explained by the presence of one or more cytochrome P-450 species induced by exposure to PAH-type compounds in the livers of the fish with AHH activity above this value. The occurrence of a polypeptide species of the same MW (57 000) in hepatic microsomes of both PAH-treated flounder (Fig. 2) and untreated flounder with high hepatic AHH, and its relative diminution in flounder with lower AHH activities, supports the concept of cytochrome P-450 induction due to environmental exposure to PAH or PAH-like compounds. To our knowledge this is the first report showing a polypeptide band of similar MW from hepatic microsomes of PAH-treated fish and untreated wild fish (Fig. 3). GST and GT activities are also induced by PAH and PAH-like compounds in mammalian species (Kaplowitz et al. 1975; Bock et al. 1978). Induction of these activities in flounder with elevated AHH activity would lend support to the concept that many of these flounder had environmental exposure to PAH or PAH-like compounds. However, in the untreated fish examined, there was no apparent relationship of either of these activities to hepatic AHH activities (Table 5). The induction of GT by βNF treatment demonstrates that the flounder enzyme is responsive to PAH-like compounds, however. The lack of a GST response is not surprising since this requires large PAH doses, even in mammals.

It is feasible that inducing agents sequestered in the liver would partition into the blood and distribute into other tissues, possibly causing enzyme induction in these other sites. Alternatively, induction might occur in a tissue important for uptake or even elimination of the inducing chemical(s). However, this did not appear to be the case in these fish as there was no relationship between renal or gut AHH activities and hepatic AHH activities in the untreated fish examined (Table 6) although it is clear that βNF caused induction of renal, but not intestinal, AHH activity in this marine teleost.

If PAH-type marine pollutants contribute to the variation of hepatic AHH activity in winter flounder, then fish from areas with higher pollution might be expected to show a higher number of fish with hepatic AHH activity of an induced character (i.e. high AHH activity inhibited by ANF). Our data are consistent with this concept. More than 90% of the flounder captured near Newport, Rhode Island, an industrialized area relative to Mt. Desert Island, had hepatic AHH activities which were inhibited by ANF. However, only a limited number of Rhode Island fish were sampled.

The physical characteristics of the fish studied explain only a small amount of the variability of the hepatic AHH activities and thus cannot be considered as causal of the variation (Table 7). Spawning has been reported by other workers to affect hepatic AHH activities in male trout (Stegeman and Chevion 1980), but our experiments were not comparable to these because Maine winter flounder finish spawning in early May (Klein-MacPhee 1978).

It is not likely that the observed variation has as its basis an "Ah locus" analogous to that elegantly demonstrated in mice (Nebert et al. 1975). In our studies, all fish treated with PAH were induced by the biochemical criteria employed (i.e. high hepatic 7-ERD activities and high hepatic AHH activities which were inhibited by ANF). Pederson et al. (1976) speculate that gene redundancy may account for the variation in hepatic AHH activities they observed in geographical subspecies of rainbow trout (*Salmo gairdneri*). However, the properties of the cytochrome(s) P-450 responsible for AHH activity in this species were not determined. In any event, the migratory habits of winter flounder and the limited area of capture we used argue against a mixing of geographical subspecies. Winter flounder are considered to be one of the least migratory fish in North America, being composed of local independent populations (Smith 1975). However, the fact that such variation in hepatic AHH and 7-ERD activities seems, at least to date, to occur exclusively in teleosts may indicate the existence of genetic factors that predispose teleosts to such variations (Gruger et al. 1977; Pederson et al. 1976; James et al. 1979).

An environmental basis for the large variation in hepatic AHH and 7-ERD activities in winter flounder is strongly supported by the biochemical similarities of liver from untreated flounder with high hepatic AHH activities to those livers from fish induced by treatment with PAH (Fig. 2 and 3). Since none of the flounder tested were "nonresponsive" to PAH administration (Table 4), the differences or variations of these activities are likely related to dose and responsiveness of the individual fish. Thus, through different habits, fish may be exposed to varying amounts of PAH-type inducing agents. As a demersal fish, spending nearly their entire lives burrowed into sediment (Klein-MacPhee 1978), the possibility of environmental interaction between the flounder and contaminants within sediments is maximized. Bottom sediments are now generally recognized as the final repository of various petroleum pollutants (Vandermeulen and Gordon 1976; Cretney et al. 1980) and often contain appreciable amounts of PAH (Laflamme and Hites 1978). Considerable evidence exists demonstrating the uptake and bioaccumulation of aromatics from sediments by demersal flatfish (McCain et al. 1978; Varanasi and Gmur 1981). This concept is also supported by recent work from our laboratory (Fisher et al. 1983) which demonstrates that three species of non-demersal flatfish caught in the same area of Maine as these flounder show no evidence of PAH-induced hepatic monooxygenase activities.

Even if the induction of the hepatic monooxygenase systems in many of these flounder is the result of environmental exposure to inducing agents, it must be stressed that the causative agents of this induction cannot be limited to PAH. As demonstrated here in flounder and elsewhere in trout (Elcombe and Lech 1979), the biochemical characteristics of teleost hepatic monooxygenase systems which are induced by certain flavonoids and PCB isomers are indistinguishable from those caused by induction with PAH. Due to the ubiquity of PCBs and PAH, it is possible that exposure of wild teleost populations to low levels of these chemicals is unavoidable. Organochlorines, including PCBs, and organic mercurials were found in tissues of marine species collected near Mt. Desert Island, Maine (Guarino et al. 1974, 1976; Pritchard et al. 1973). PAH were also analyzed in sediments from Casco Bay, just south of Mt. Desert Island (Larsen et al. 1983). Detectable amounts of PAH were present at all stations (n = 30), and concentrations in "pristine" areas varied 3- to 4-fold, indicating multiple sources for these pollutants. Thus, known PAH-type inducers (certain PCB isomers) are known to be present in species sampled near Mt. Desert Island, and

by analogy with Casco Bay, PAH are likely to be heterogeneously distributed in marine sediments in the area. There is also evidence for the presence of flavones and flavonoid compounds in terrestrial plants and in at least 43 different species of sea grasses (McMillan et al. 1980). Other compounds of botanic origin which induce monooxygenase activity in mammals include safroles and indoles (Wattenberg et al. 1976). Thus, the biological response in these flounder may be elicited by compounds synthesized by marine plants, by several different classes of anthropogenic chemicals or by a combination of chemicals from each source.

Acknowledgments

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Length Changes in Silver Hake (*Merluccius bilinearis*) Larvae: Effects of Formalin, Ethanol, and Freezing

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Silver hake (*Merluccius bilinearis*) larvae preserved in either formalin or ethanol decreased in length over time, most shrinkage being achieved in the first 15 d. The magnitude and variability of the length reduction was greater for smaller larvae. Rate and magnitude of shrinkage for ethanol-preserved larvae exceeded those of formalin-preserved larvae. Frozen specimens were extremely variable in length change response, and we noted a transition from shrinkage to expansion with increasing larval length.

FOWLER, G. M., AND S. J. SMITH. 1983. Length changes in silver hake (*Merluccius bilinearis*) larvae: effects of formalin, ethanol, and freezing. Can. J. Fish. Aquat. Sci. 40: 866–870.

Les larves de merlu argenté (*Merluccius bilinearis*) conservées soit dans la formaline, soit dans l'éthanol, rétrécissent avec le temps, la plus grande partie du rétrécissement se produisant durant les premiers 15 jours. L'ampleur et la variabilité de cette diminution de longueur sont plus prononcées chez les petites larves. Le taux et l'ampleur du rétrécissement des larves conservées dans l'éthanol sont plus importants que ceux des larves conservées dans la formaline. Le changement de longueur de sujets congelés est extrêmement variable, et on observe une transition du rétrécissement à l'expansion à mesure qu'augmente la longueur larvaire.

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FIXATION and preservation techniques are known to cause changes in the length, weight, and quality of larval samples for a number of fish species, necessitating the use of adjustments to convert from preserved to fresh measurements. Most of the work to date has concentrated on the effects of various formalin solutions in relation to preservation time and larval size (Blaxter 1971; Hay 1981, 1982; Lockwood and Daly 1975; Parker 1963; Rosenthal et al. 1978; Schnach and Rosenthal 1978; Theilacker 1980). These studies demonstrated a reduction in the lengths of the larvae, the magnitude of which was dependent upon the duration of storage and the initial lengths of the specimens. The preservation effects of ethanol have received less attention than formalin (Radtke and Waiwood 1980; Theilacker 1980). Radtke and Waiwood found that for Atlantic cod (*Gadus morhua*), preservation in ethanol resulted in age-dependent reduction in larval lengths whereas Theilacker concluded that there was no effect at all for northern anchovy (*Engraulis mordax*). Freezing has not been investigated previously with respect to its effects on larval morphometrics, although its effects on adults have been studied (Engel 1974; Halliday and Roscoe 1967).

Our objective was to study the effects of the three preservation treatments on the lengths of larval silver hake (*Merluccius bilinearis*) specimens. This information is necessary if larval lengths obtained from preserved specimens are used to provide age and growth parameters for stock assessment purposes.

Methods

Silver hake larvae were obtained from 10- to 20-min oblique bongo tows (333-μm mesh) during the Scotian Shelf Ichthyoplankton Program cruise AR02 (*Argus*, Sept. 3–29, 1980). Standard length (tip of upper jaw to end of notochord) of each larva was measured by a precalibrated ocular micrometer to 0.1 mm, within 10–15 min of capture. Subsequent measurements (postpreservation) were accurate to 0.05 mm, the greater precision achieved in the absence of vessel movements. Larvae were randomly allotted to three preservation treatments: 4% neutral formalin–seawater (31–32‰) solution, 95% ethanol, and freezing in petri dishes on wetted filters. Identification of individual specimens was maintained by the use of numbered vials and filter papers. Sample sizes of eighty-three individuals were subjected to each treatment. Size ranges were 3.7–14.4 mm (formalin), 3.2–16.8 mm (ethanol), and 4.6–41.0 mm (frozen), with most of the speci-

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TABLE 1. Average percent shrinkage of silver hake larvae with time. Values in parentheses denote mean lengths (mm) of treatment groups.

	n	Range of initial lengths (mm)	15 d (T_1)	30 d (T_2)	50 d (T_3)	T_4[a]
Formalin	83	3.7–14.4 (8.50)	3.4 (8.21)	3.7 (8.18)	3.6 (8.19)	4.3 (8.14)
Ethanol	83	3.2–16.8 (9.78)	4.8 (9.30)	5.6 (9.25)	6.0 (9.23)	7.0 (9.16)
Freezing	83	4.6–41.0 (9.48)	—	—	—	1.4 (9.44)

[a] T_4 = 337 d (formalin), 205 d (ethanol), and 338 d (freezing).

TABLE 2. Statistical analysis of percent shrinkage results obtained from formalin and ethanol treatments of silver hake larvae.

Hypothesis tested		Test statistic (observed F)	Degrees of freedom	P level
1) Parallelism: formalin vs. ethanol[a]		10.44	3,162	$P<0.0001$
2) Equality treatment means		N/A[b]		
3) Equality of effects over time:				
a) Formalin		77.79	4,79	$P<0.0001$
Contrasts	T_0-T_1	17.76	4,79	$P<0.0001$
	T_1-T_2	3.31	4,79	$0.01<P<0.05$
	T_2-T_3	1.13	4,79	$0.30<P<0.35$
	T_3-T_4	3.71	4,79	$0.005<P<0.05$
b) Ethanol		92.96	4,79	$P<0.0001$
Contrasts	T_0-T_1	14.14	4,79	$P<0.0001$
	T_1-T_2	2.66	4,79	$0.01<P<0.05$
	T_2-T_3	0.68	4,79	$0.60<P<0.65$
	T_3-T_4	7.16	4,79	$P<0.0001$

[a] Tested for comparable times (T_0, T_1, T_2, T_3).
[b] Because parallelism was rejected at $\alpha = 0.001$, a test of this hypothesis is meaningless (see text).

mens in the 4- to 15-mm range for all treatments. Ethanol samples were remeasured at 15, 30, 50, and 205 d following fixation. One or two drops of distilled water were applied to specimens on the slide to counteract the dehydrating effect of rapid evaporation of ethanol. Formalin samples were remeasured at 15, 30, 50, and 337 d. No compensation for dehydration was believed necessary for formalin-preserved larvae. In both cases 20–30 s elapsed between removal and return of larvae to their vials. The frozen samples were maintained at a temperature of about −15°C for a period of 338 d, thawed with distilled water, and measured. Repeated thawing and refreezing would damage the specimens, rendering observations at discrete time intervals useless.

The length measurements were expressed in terms of percent shrinkage, defined as

$$\left(1 - \frac{\text{length at time } T}{\text{initial length}}\right) \times 100$$

for each specimen. Results from the formalin and ethanol treatments were analyzed by a repeated measures approach which incorporates temporal correlation between measurement intervals into the test statistics. Details of the test statistics are discussed by Morrison (1976, sections 4.5 and 4.6).

Results

The average percent shrinkage results obtained from the preservation experiment are presented in Table 1.

In Figures 1, 2, and 3, box and whisker plots are used to present final percent shrinkage results relative to the initial lengths of the larvae (arbitrarily divided into 2-mm groups). The upper and lower edges of the boxes in the figures mark the positions of the upper and lower quartiles, respectively, with the position of the median indicated by an asterix. The dotted lines (whiskers) join the upper and lower extreme values to the boxes. For further information on this type of plot see Tukey (1977) and Reckhow (1980).

We followed the analysis hierarchy described in Morrison (1976; p. 153–154); the results of the statistical test are presented in Table 2. Because the null hypothesis of parallelism between ethanol and formalin treatments was rejected, we can conclude that the two preservatives do not affect larval shrinkage in a similar manner over time. As a further test of equality of treatment means would be meaningless, the results were analyzed separately for each treatment.

For larvae preserved in formalin an average percent shrinkage of 4.3 (range = 0.0–14.8%) was observed after 337 d. The most significant reduction in length occurred during the first 15 d (Table 2) with the mean larval length continuing to

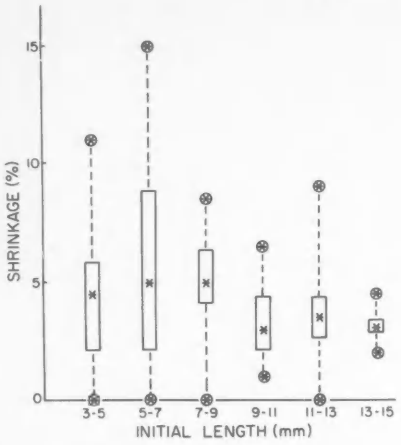

FIG. 1. Box and whisker plot of percent shrinkage results of formalin-preserved silver hake larvae at T_4 (337 d) relative to initial larval lengths. (* = position of median. See text for explanation.)

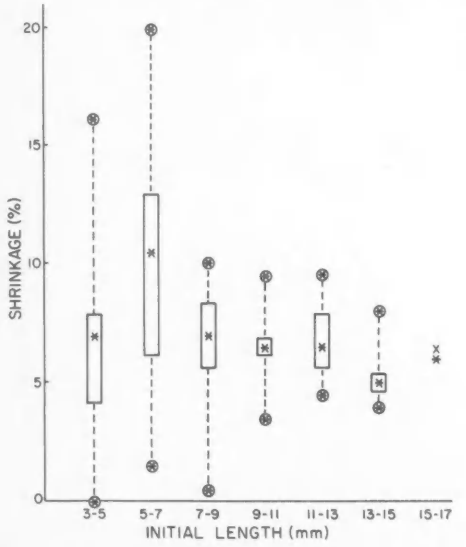

FIG. 2. Box and whisker plot of percent shrinkage results of ethanol-preserved silver hake larvae at T_4 (205 d) relative to initial larval length. (* = position of median, x = position of observations when three or fewer points were available. See text for explanation.)

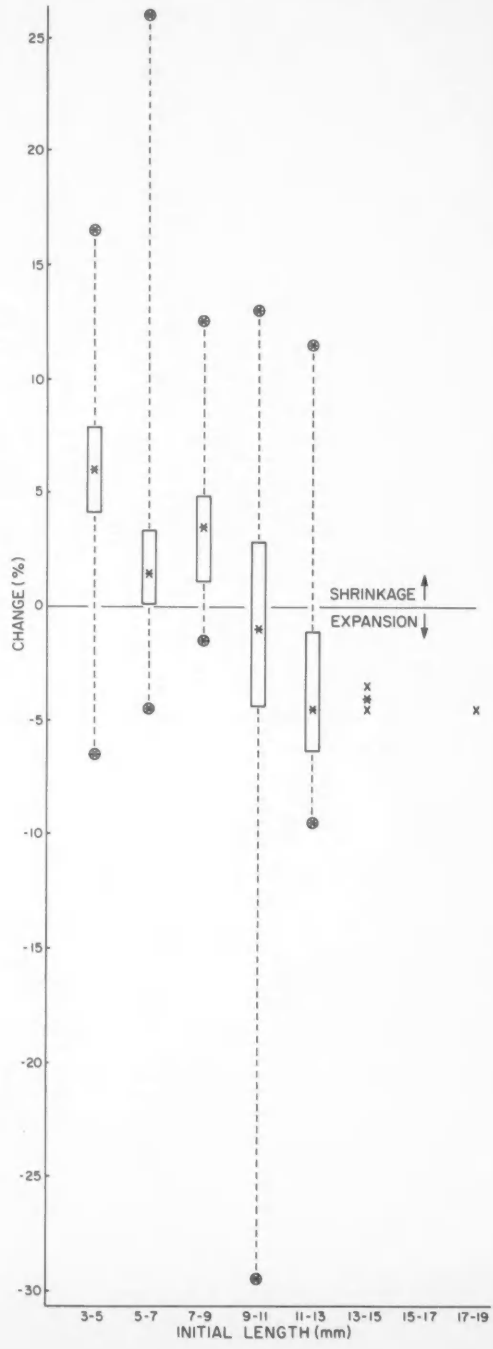

FIG. 3. Box and whisker plot of percent shrinkage results of frozen silver hake larvae at 338 d relative to initial larval length. (* = position of median, x = position of observations when three or fewer points were available. See text for explanation.)

shrink for the duration of the experiment, but at a slower rate. The increase in significance of the test statistic for the final contrast (T_3–T_4) relative to the previous contrast reflects the longer time interval involved rather than a sudden increase in shrinkage. In addition to the temporal effects there was also a relationship between treatment response and initial larval length. Figure 1 indicates that the median percent shrinkages for larvae greater than 9 mm initial length were less than those for smaller larvae. Larvae greater than 7 mm exhibited less variability than smaller larvae, this variability being measured by comparing the lengths of the boxes (i.e. interquartile range). The largest interquartile range and range of extreme values occurred for larvae in the 5- to 7-mm group.

Ethanol-preserved larvae had a mean shrinkage of 7.0% (range = 0.0–20.0%) after 205 d. Though the greater part of this reduction occurred in the first 15 d, shrinkage from day 50 to day 205 was highly significant (Table 2) despite the declining rate of shrinkage over time. With respect to initial length Fig. 2 demonstrates that there was larger variation associated with the response of the smaller larvae (less than 7 mm) and a gradual decrease in shrinkage with increasing larval size. The highest median percent shrinkage and variability was exhibited by larvae in the 5- to 7-mm group.

The estimate of 1.4% shrinkage for frozen samples at 338 d was derived from length changes which ranged from −29.9% (expansion) to +26.5% (reduction). The highly variable nature of length response to freezing is depicted in Fig. 3. Larvae which were greater than 19 mm are not included in this figure because no change in length was observed. A transition in median response from shrinkage to expansion as larval size increases is also evident in this figure.

Discussion

Preservation in Formalin

The observation that larval silver hake shrink over time when preserved in formalin with the greater part of this shrinkage occurring in the first few days is consistent with findings reported for other species (Blaxter 1971; Lockwood and Daly 1975; Schnack and Rosenthal 1978; Hay 1981, 1982). In addition the tendency for the magnitude of shrinkage to decrease with increasing initial larval length has also been observed by Lockwood and Daly (1975), Schnack and Rosenthal (1978), and Hay (1981, 1982).

However, Theilacker (1980), in noting for laboratory-reared northern anchovy larvae that capture/handling stress (including death) was chiefly responsible for larval shrinkage, further concluded that size-dependent shrinkage was a consequence of handling alone and not preservation. This conclusion was based on a comparison of ratios of posttreatment lengths to pretreatment lengths of larvae after (1) preservation in formalin, (2) simulated net-capture, and (3) preservation after net-capture. The inconsistency between Theilacker's results and those of other studies may be explained by the shorter duration time of preservation in her experiment. As Schnack and Rosenthal (1978) and Hay (1982) have noted for Pacific herring (*Clupea harengus pallasi*), size-dependent shrinkage becomes more pronounced the longer the larvae are stored in formalin. The difference may also be due to a species-specific response, as Lockwood and Daly (1975) found that larval dabs (*Limanda limanda*) and plaice (*Pleuronectes platessa*) react differently to storage in formalin.

The observation with silver hake larvae of an increase in variability of the shrinkage response with decreasing larval size has not been mentioned as occurring in previous investigations of preservation shrinkage, possibly because of the limited range of lengths treated in other studies. The only exception is Theilacker's study, which covered as wide a size spectrum as ours did but only reported averaged results for smaller larvae such that the degree of variation present could not be evaluated.

Preservation in Ethanol

Significant reduction in length and decreasing magnitude of shrinkage with increasing initial length for larvae preserved in ethanol was found both in our experiment with silver hake and for cod (posthandling lengths vs. postpreservation lengths, data pooled by us) in Radtke and Waiwood (1980). The change in variability of response with size could not be compared for cod data because that study concentrated on very small larvae (4.27–5.62 mm). Theilacker (1980) examined the effects of ethanol on simulated net-caught and laboratory-reared northern anchovy larvae in the same manner as she did for formalin. She concluded that ethanol did not cause larvae to shrink. However, it was not possible for us to evaluate these findings because no data were presented for net-treated specimens.

Neither the cod nor the anchovy studies looked at duration effects of ethanol. Our observations then, that larvae preserved in ethanol undergo increasing magnitude but decreasing rate of shrinkage over time cannot be compared with these investigations.

Comparison of Formalin and Ethanol

For silver hake larvae both treatments exhibited decreasing rates of shrinkage over time with most of the length reduction occurring in the first 15 d and decreasing percent shrinkage and variability of response with increasing size of larvae. Size-dependence in this relationship was likely a function of increased rigidity of larger specimens due to ossification, much as Theilacker (1980) suggested to explain shrinkage differences resulting from capture alone. The greater rate of shrinkage noted for the first 15 d relative to the later periods we believe attributable to continuing autolysis prior to tissue saturation with preservative, and to tissue degradation during the more pronounced osmotic changes of newly preserved samples. The greater rate and magnitude of shrinkage with the ethanol-preserved samples constitutes the major difference between the two treatments. It was also noted that larvae preserved in ethanol were firmer than those in formalin and more faded in coloration (most notably the color of the stomach).

Freezing

Larvae demonstrated extreme variability in length change response to freezing, being easily stretched or compressed without visible structural damage. Thus it is our opinion that

freezing is an unsuitable method for preserving fragile larval samples for length-related analyses.

Implications to Abundance/Mortality Estimates

Length measurements from preserved larvae have been used to obtain mortality and recruitment estimates for commercial fish stocks (e.g. Lough et al. 1980), but given the results of this and other studies such practices may have significant ramifications. Where measurements are equated to predetermined length at age estimates and applied to growth/mortality formulae, underestimation of age due to larval shrinkage could result in overestimation of mortality, especially if no allowance is made for capture-induced shrinkage. The lower recruitment estimates derived from length data without adjusting for shrinkage may thus bias predictions of stock abundance and hence influence potential yield determinations. This bias might explain intances of stock abundance estimates from larval surveys falling short of virtual population assessment estimates, as noted in Lough et al. (1980).

Practical Considerations and Suggestions

The use of preserved samples to derive larval length data is statistically risky because of the extent and variability of length changes resulting from stress and preservation. Nor would measurements of freshly caught larvae alleviate the problem as many authors report that the influence of capture and handling alone is of greater magnitude than any subsequent changes during preservation. But where rough estimates of larval lengths of wild populations are desired, and measuring feasibility and precision under land-based laboratory conditions is significantly superior to shipboard attempts, it becomes necessary to develop the best methods possible to obtain and analyze preserved larval samples.

We believe freezing to be a very poor preservation technique where larval length estimates are required due to the unpredictability of individual length changes. In choosing between formalin and ethanol, it might be argued that formalin is the better option by virtue of the lesser rate of shrinkage and greater abundance of previous data in the literature available for comparison. With respect to measurement, however, the firmer specimens obtained by preservation in ethanol might be more desirable provided a 95% concentration of the solution is consistently achieved to avoid the destructive lower pH levels of less concentrated solutions (K. Waiwood, Fisheries and Oceans, Biological Station, St. Andrews, N.B., personal communication). It is also the best choice when correlations between larval length and the growth rings of otoliths are required, as formalin dissolves calcium. Should ethanol be preferred it would be advisable to generate a background of experimental data to provide consistent estimates of shrinkage with the preservative. In either case the nature of the preservation responses are essentially the same. Larvae undergo most of their shrinkage within a few days, after which shrinkage continues but at a much lesser rate. Magnitude of shrinkage increases as the initial size of larvae decreases, likely a function of greater rigidity of body structure with maturity (Radtke and Waiwood 1980). Coupled with this relationship we expect an increase in variability of length change response to preservation with decreasing larval size.

Where length data is to be obtained from preserved samples, we propose a waiting period of at least 50 d between collection and measurement to avoid the more dynamic shrinkage trends of recently stored samples. Furthermore, the problem of response variability observed with small larvae must be approached cautiously. If possible, the appropriate size range should be dealt with separately, as a single class, while applying a different method to larger specimens. Any loss in continuity must be weighed against the loss in precision of length estimates over the larger size range.

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Tidal Mixing and Summer Plankton Distributions in Hecate Strait, British Columbia

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Perry, R. I., B. R. Dilke, and T. R. Parsons. 1983. Tidal mixing and summer plankton distributions in Hecate Strait, British Columbia. Can. J. Fish. Aquat. Sci. 40: 871 – 887.

Summer plankton distributions in Hecate Strait, northern British Columbia, were examined during 1979 and 1980 and compared with tidal mixing characteristics. Calculations of the Simpson–Hunter tidal stratification parameter ($h \cdot U^{-3}$) indicate that most of Hecate Strait is potentially stratified in summer (in the absence of excessive storms), with a well-mixed region over the shallow shelf adjacent to the Queen Charlotte Islands. Vertical temperature profiles collected from a coastal oil tanker ship of opportunity confirmed the presence of mixed and stratified water masses as predicted. Near-surface concentrations of chlorophyll *a*, nutrients, diatoms, and copepods were lower in the mixed region (<1 μg Chl. $a \cdot L^{-1}$) than the statified region, but highest (5 μg Chl. $a \cdot L^{-1}$) at the front between these mixing regimes. We believe that low phytoplankton biomass in western mixed waters is due to nutrient rather than light limitation, whereas possible advection of nutrients along the edge of the western shelf may support the higher biomass of the frontal region. Such a frontal zone is likely important to groundfish production in this region.

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La distribution estivale du plancton dans le détroit d'Hécate, au nord de la Colombie-Britannique, a été étudiée en 1979 et 1980, et comparée avec les caractéristiques de mélange de marée. Les calculs du paramètre de stratification de marée de Simpson–Hunter ($h \cdot U^{-3}$) indiquent que la majeure partie du détroit d'Hécate est potentiellement stratifiée en été (en l'absence de tempêtes excessives), avec région bien mélangée au-dessus du plateau peu profond adjacent aux îles Reine-Charlotte. Les profils de température verticaux recueillis par un pétrolier côtier disponible dans la région confirment la présence de masses d'eau mélangées et stratifiées, telles que prédites. Près de la surface, les concentrations de chlorophylle *a*, de nutriments, de diatomées et de copépodes sont plus faibles dans la région de mélange (<1 μg Chl. $a \cdot L^{-1}$) que dans la région stratifiée, mais sont à leur maximum (5 μg Chl. $a \cdot L^{-1}$) au front séparant ces régimes de mélange. Nous croyons que la faible biomasse phytoplanctonique dans les eaux mélangées de l'ouest est due à une limitation des nutriments plutôt que de la lumière, alors que l'advection possible de nutriments le long de la marge du plateau occidental peut supporter la biomasse plus grande de la région frontalière. Cette dernière joue probablement un rôle important dans la production de poissons de fond dans ce secteur.

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Hecate Strait, a coastal seaway in northern British Columbia, is poorly known biologically yet supports important fishery resources and salmonid migration routes. A few studies have discussed zooplankton distributions in the strait, either in very general reviews of the northeast Pacific (LeBrasseur 1965), from results of fish stomach content analyses (Manzer 1969), or localized studies of specific inlets and regions of the northern B.C. coast (Cameron 1957; Gardner 1982a). However, no data are available concerning the distribution of phytoplankton spatially or seasonally in Hecate Strait. In this study, our purpose was to investigate plankton distributions in Hecate Strait during summer 1979 and 1980 using a coastal oil tanker as a ship of opportunity, and to consider the influence of tidal mixing as an important mechanism regulating these distributions.

The tidal front model proposed by Simpson and Hunter (1974) identifies well-mixed and stratified regions in a given area, separated by a boundary or front. Those combinations of tidal velocity and water depth producing mixed and stratified regions, under a constant heat flux, can be identified using the

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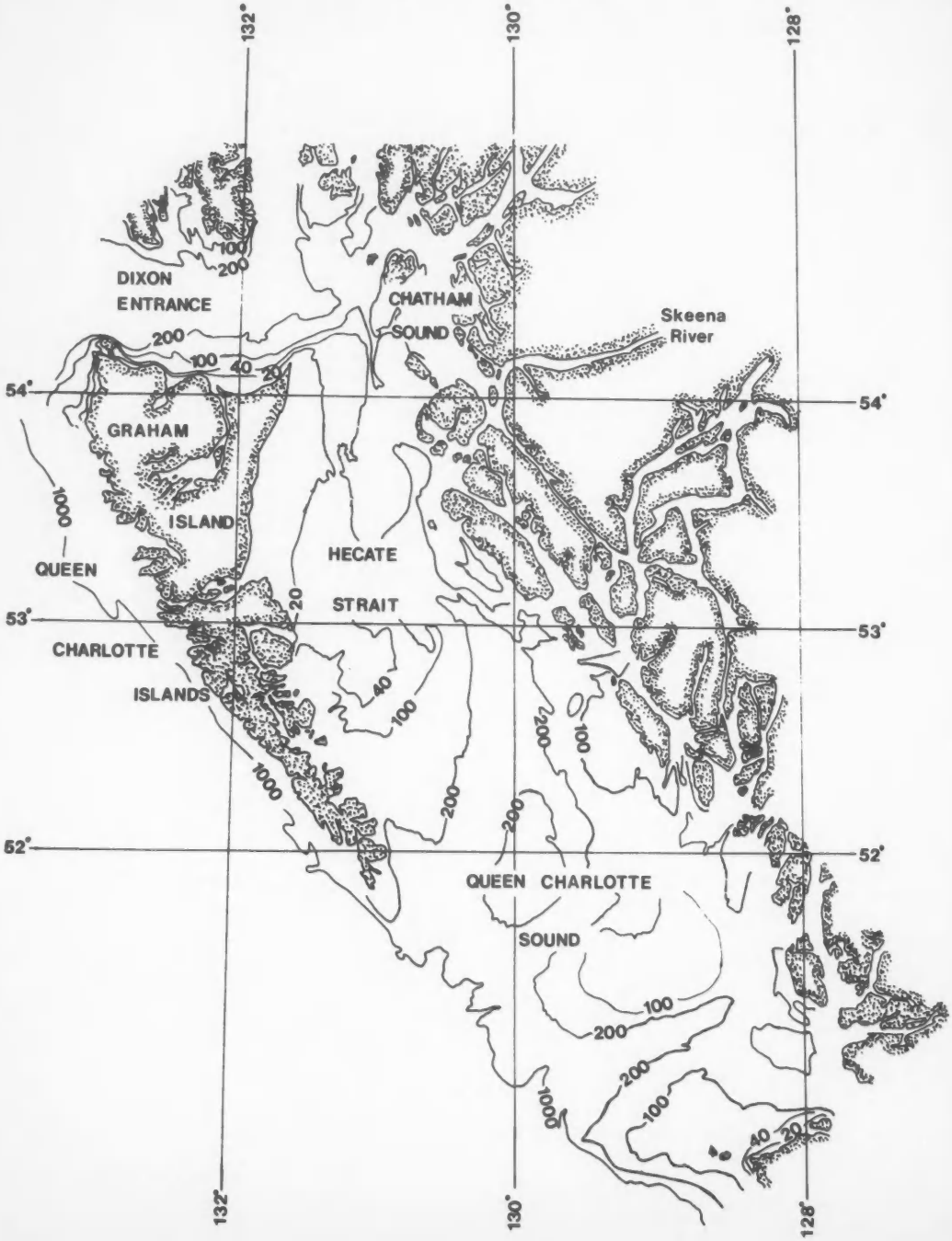

132°
130°
128°
DIXON
ENTRANCE
CHATHAM
SOUND
Skeena
River
54°
GRAHAM
ISLAND
QUEEN
CHARLOTTE
ISLANDS
HECATE
STRAIT
53°
52°
QUEEN CHARLOTTE
SOUND
100
200
40
20
1000

equation

$$S = \log_{10}\left[\frac{h}{C_d|\bar{U}|^3}\right].$$

As described by Pingree (1978), S is the stratification parameter, h the depth of the bottom, C_d a bottom drag coefficient, and $|\bar{U}|$ the magnitude of the instantaneous tidal stream velocity averaged over one tidal cycle. Using a value of 0.0025 for the bottom drag coefficient C_d, the value of S (using metric cgs units) indicating a front is 1.5, with values of $S < 1.0$ representing well-mixed regions and $S > 2.0$ well-stratified regions. Field studies have confirmed the predicted locations of these fronts (Pingree et al. 1978), although they may alter position somewhat with the neap–spring tidal cycle.

Such frontal regions also have characteristic distributions of plankton and nutrients. Phytoplankton biomass and production are low on the mixed side of the front because of low mean light levels, and low on the stratified side because of nutrient exhaustion (Pingree 1978). High phytoplankton biomass and production in the frontal zone between these two regions results from a flux of nutrients across the front and a favorable light regime produced by a shallow thermocline. The associated convergent circulation patterns may also accumulate materials in the frontal region. The width of this transition zone can vary, being sharp and well-defined about the British Isles (Pingree et al. 1978) but rather diffuse and extensive among the Gulf Islands of Georgia Strait, B.C., depending on such factors as local freshwater runoff and differences in extinction coefficients (Parsons et al. 1983).

Hecate Strait (Fig. 1) is characterized by a broad shallow (<30 m) northwestern shelf near the Queen Charlotte Islands and a deep trough on the eastern side parallel to the mainland shore. This trough begins in Queen Charlotte Sound at depths of 400 m and shoals to about 75 m in northeastern Hecate Strait. To the north, Dixon Entrance forms another outlet to the Pacific, also with a deep trough shoaling to about 100 m at its eastern end. Winds in Hecate Strait tend to blow parallel to the coast, predominately from the southeast and stronger in winter (average speed 10 $m \cdot s^{-1}$, Thomson 1981) than summer, when the prevailing direction is from the northwest. Currents respond to prevailing winds, flowing northwards in winter, but more variable in summer. A summer estuarine-type circulation is quite marked in Dixon Entrance driven by runoff from the Skeena and Nass rivers, but not too important in Hecate Strait. Tides in northern British Columbia include both diurnal and semidiurnal components, co-oscillating with the adjacent North Pacific (Crean 1967). The flood tide comes north through Queen Charlotte Sound and east through Dixon Entrance, meeting in northern Hecate Strait then moving southwest towards the Queen Charlotte Islands. The tides meet in Hecate Strait 50–60 km further north in winter than in summer. The general oceanography of Hecate Strait is discussed more fully by Dodimead (1980) and Thomson (1981).

Methods

Mixed and stratified regions were determined for Hecate Strait and Dixon Entrance using the Simpson–Hunter stratification parameter (see introduction). Tidal current velocities were obtained from a two-dimensional, depth averaged numerical tidal model calculated to predict oil spill movements for the Kitimat Pipeline Project (Kinney et al. 1976). It includes the regions of Hecate Strait and Dixon Entrance between 52°N and 55°N, and 128°W and 133°W using a grid network with 9.3-km (5-nautical mile) spacing. Interpolations of the tide table data were required across the open sides of the model in Queen Charlotte Sound, Dixon Entrance, and Clarence Strait at the southern end of the Alaskan archipelago. The tidal component calculated in the model is the M2 tide with a period of 12.42 h.

The stratification parameter was calculated with h as the mean water depth averaged for each of the tide model's 9.3-km squares from Canadian Hydrographic Chart No. 3002, a bottom drag coefficient of 0.0025, and $\bar{U}$ as the mean tidal velocity for each grid position regardless of direction. To verify the existence of well-mixed and stratified zones predicted by this equation independently of tidal current and depth measurements, we calculated the stratification of surface waters for Hecate Strait and Dixon Entrance. Surface stratification was defined as the difference of σ_t between the surface and 50 m or the bottom (whichever was less), normalized per metre. Data were obtained from the Marine Environmental Data Service of Fisheries and Oceans Canada, and consisted of vertical profiles of temperature and salinity collected in Dixon Entrance and Hecate Strait during summer from 1954 to 1971.

Field data were collected as part of the University of British Columbia, Dep. of Oceanography Ship of Opportunity (SHOP) program. Methods of collection and all data obtained during the program are presented in Dilke et al. (1979) and Perry et al. (1981). Imperial Oil of Canada, Ltd. permitted use of the MV *Imperial Tofino* as a sampling platform. It is a coastal oil tanker, with a length overall of 52 m and a deadweight displacement of 1100 t. Modifications to facilitate sampling included access to the sea chest and installation of a davit and hydraulic winch at the stern for zooplankton sampling.

Stations were "occupied" while the vessel was underway between coastal settlements. Seawater for samples of salinity, nutrients, phytoplankton, and pigments was pumped from the ship's sea chest located amidships with the intake ~3 m below the sea surface depending on the ballast. The volume of the sea chest is 0.34 m^3, and with a maximum inflow of 0.091 $m^3 \cdot min^{-1}$ the residence time of seawater was about 3.75 min. Mackas and Owen (1982) have examined continuous horizontal sampling systems and have found that a system involving a sea chest can cause substantial blurring of the input signal. This makes it unable to resolve features with spatial scales less than about 0.5 km, depending on the actual configuration. Such blurring is not a problem for the sequence of discrete stations in this study, where water samples were integrated over the length of the simultaneous zooplankton tow, but can be for continuous transects of temperature and fluorescence.

FIG. 1. Bathymetric map of the northern B.C. coast showing locations of geographic features referred to in the text. Bathymetric contours are in metres.

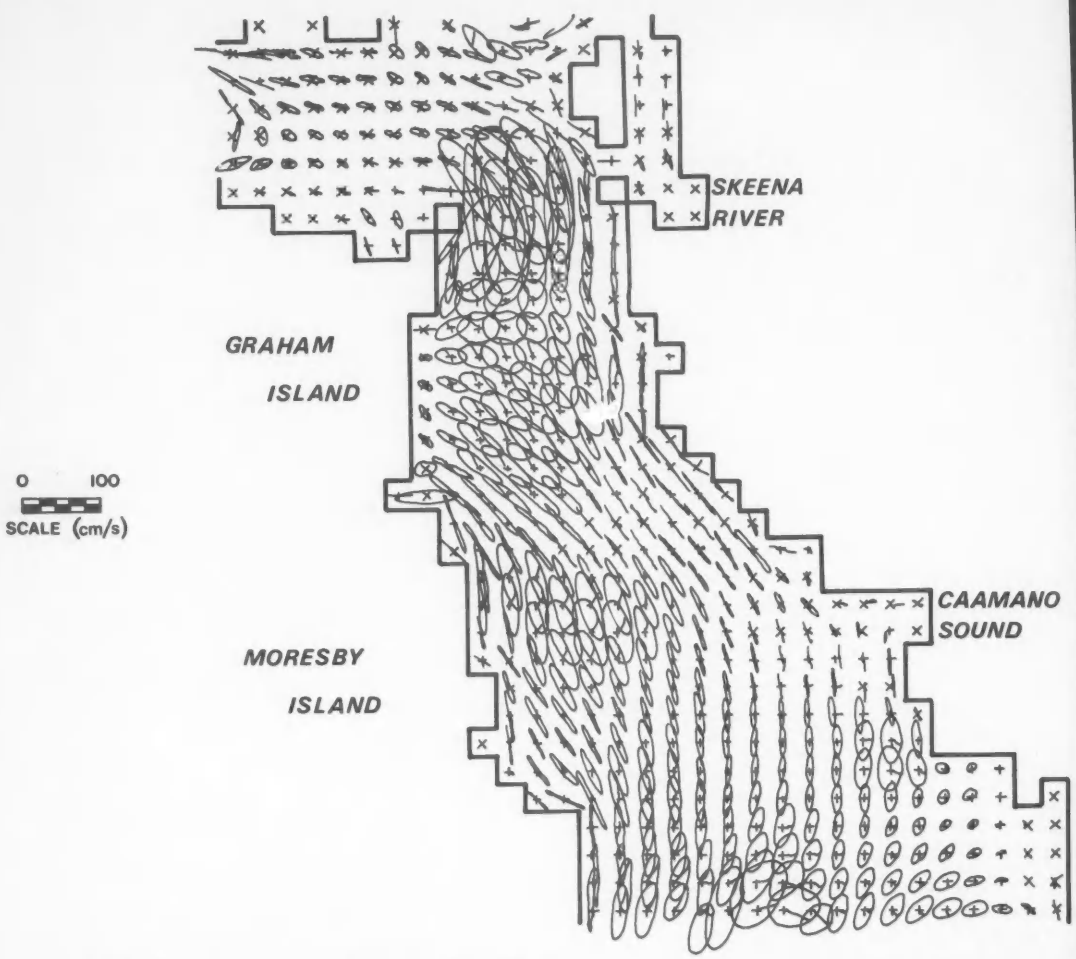


FIG. 2. Tidal current ellipses computed from the oil spill drift prediction model for Hecate Strait and Dixon Entrance. Redrawn with permission from Kinney et al. (1976).

Phytoplankton samples were preserved with Lugol's solution and identified to genus or taxonomic size group using the inverted microscope technique of Utermöhl (1958). Chlorophyll *a* and pheopigments were determined on shore by the fluorometric method outlined in Strickland and Parsons (1972). Nutrient samples were first filtered through Gelman type A/E filters to remove particulate matter, then collected in plastic bottles and frozen. On shore, analyses for nitrate plus nitrite, phosphate, and silicate were done with a Technicon Auto Analyser as described in Strickland and Parsons (1972). As these nutrients covaried on the cruises, results are reported for $NO_3 + NO_2$ only. Lower limit of detection was 0.10 μmol $NO_3 \cdot L^{-1}$.

Surface temperature at each station was measured underway with a modified bucket sampler. Vertical profiles of temperature were obtained with an expendable bathythermograph (XBT) system.

Zooplankton were sampled using a high-speed Miller sampler (Miller 1961) fitted with a 350-μm mesh net towed horizontally at about 3 m depth to match the ship's intake. A typical tow would last 10 min, with the volume of water filtered determined from a calibrated flowmeter installed within the body of the sampler. Results are reported as numbers of organisms, and are divided into copepods and all zooplankton excluding copepods (termed noncopepod zooplankton). Zooplankton were not sampled from every station.

Near-surface chlorophyll fluorescence was measured continuously across Hecate Strait in June, 1980 (cruise 14)

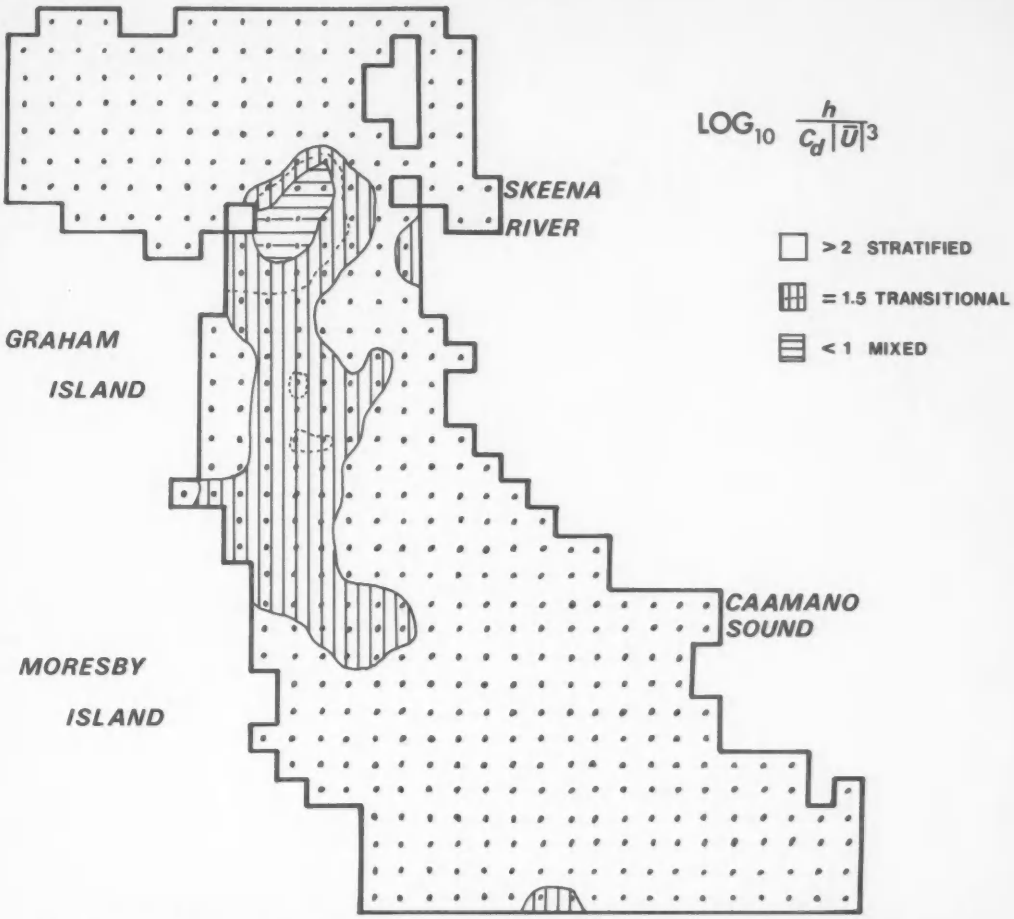


FIG. 3. Calculations of the Simpson–Hunter stratification parameter, with h the depth of the water, $\bar{U}$ the tidal current velocity averaged over one tidal cycle (both cgs units), and a drag coefficient (C_d) of 0.0025. Values for stratified, transitional, and mixed zones are from Pingree (1978). Dots represent data locations.

and both fluorescence and temperature were measured on cruise 15 in August, 1980. Water samples were collected on cruise 14 at intervals to measure extracted chlorophyll *a* concentrations. For cruise 15, results are presented as relative fluorescence as an insufficient number of samples were collected to permit conversion to chlorophyll. Bathymetry of the August transect was obtained from Canadian Hydrographic Chart No. 3002, with a digitizing interval of 15 min. The strip chart output record of continuous fluorescence and temperature from cruise 15 was digitized with a 3-min interval.

Results

Tidal ellipses for Hecate Strait computed by the tide model are presented in Fig. 2. The largest ellipses (computed currents up to 0.75 $m \cdot s^{-1}$) occur off the northeast coast of Graham Island. However, Thomson (1981) has noted there can be considerable distortion of tidal streams near broken shorelines in the area that would not be indicated by a model with 9.3-km grid spacing. Any sharp localized discontinuity of the bathymetry would similarly not be represented.

Comparison of the tidal ellipses (Fig. 2) with the bathymetry (Fig. 1) shows the greatest tidal current velocities occur over the shallowest banks of Hecate Strait. Calculation of the stratification parameter for Hecate Strait and Dixon Entrance also indicates this to be a region of intense vertical mixing, surrounded by a transition zone (S between 1 and 2) of varying width, whereas the remainder of the strait is potentially stratified during summer (Fig. 3). Sharpest horizontal gradients of mixing occur between Dixon Entrance and Hecate Strait, and between Graham Island and Chatham

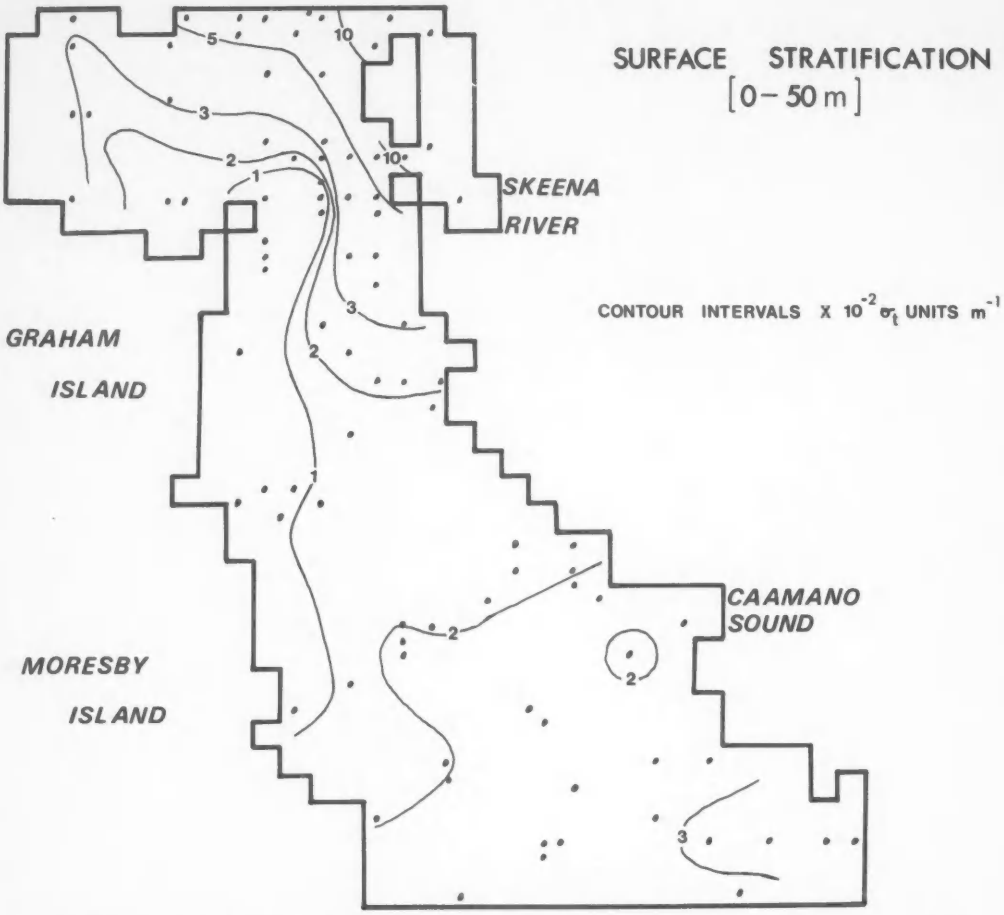


FIG. 4. Surface stratification, the density difference from the surface to the bottom or 50 m (whichever is less) normalized per metre, for Hecate Strait and Dixon Entrance. Data presented are a composite of June, July, and August calculated from temperature and salinity measurements in the region from 1954 to 1971. Dots represent data locations.

Sound, coinciding closely with changes of bathymetry. These are locations where fronts could be expected, being the boundary between well-mixed and stratified water masses.

For comparison with the Simpson–Hunter stratification parameter, surface stratification values are grouped into the same 9.3-km squares used for the tidal calculations and contoured (Fig. 4). Although the sampling density is much less than for the tidal stratification parameter, the comparison of mixed and stratified regions is good. Surface stratification values over shallow western Hecate Strait are less than 0.01 σ_t units·m^{-1}, indicating well-mixed conditions, whereas eastern Hecate Strait is more stratified with values greater than 0.03 σ_t units·m^{-1}. As with the tidal stratification calculations, the sharpest gradient of surface stratification occurs in northern Hecate Strait. The influence of the Skeena River is also clear, with the surface stratification of eastern Dixon Entrance well over 10 σ_t units·m^{-1} and the contour lines indicating the general north and westward flow. Correlations of the two measures of stratification for the grid squares in which they coincide are

	June to August inclusive	June	July	August
Correlation coeff.	0.37	0.40	0.30	0.49
Significance	0.00	0.00	0.08	0.00
Number of observations	168	86	42	40

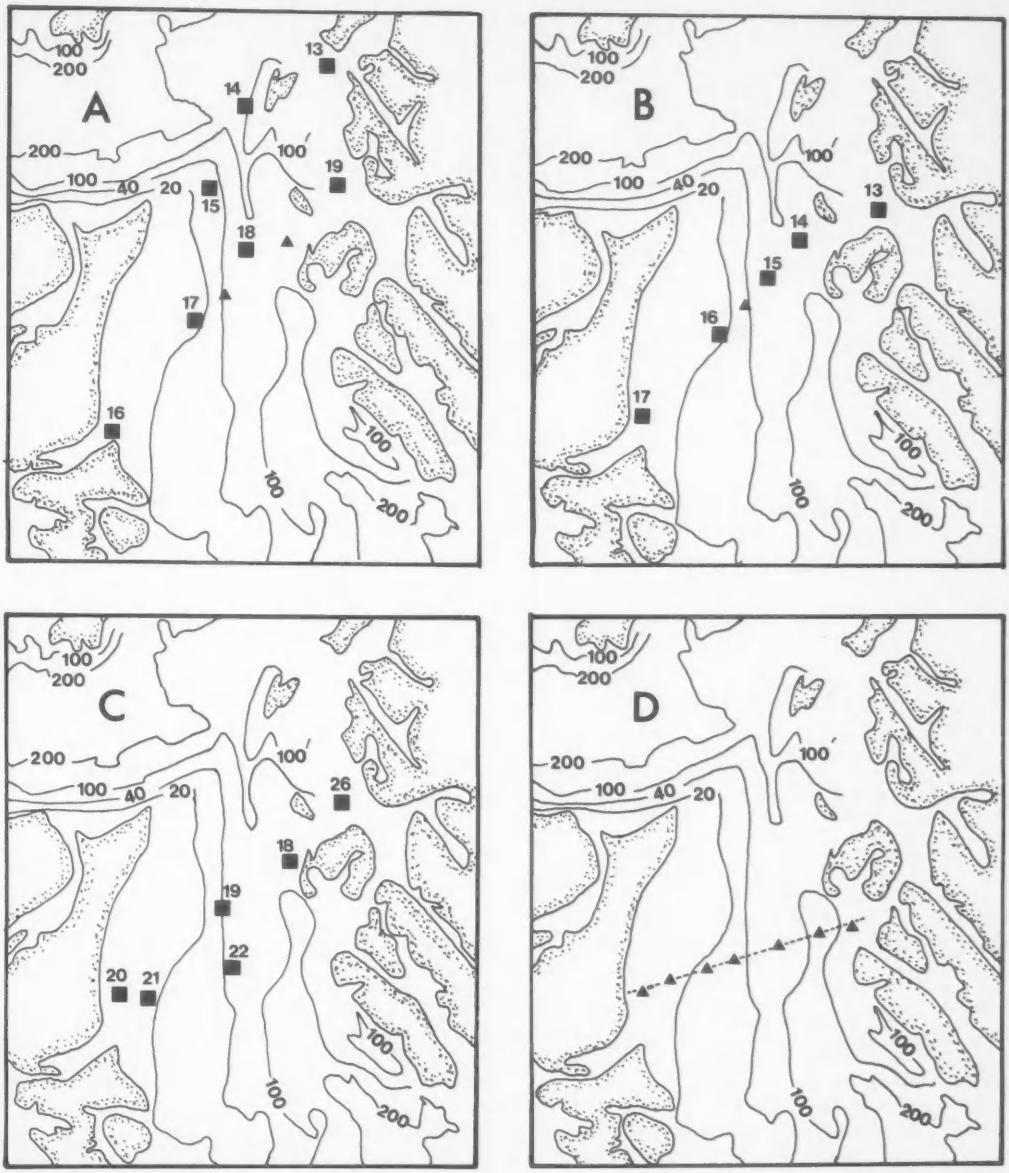
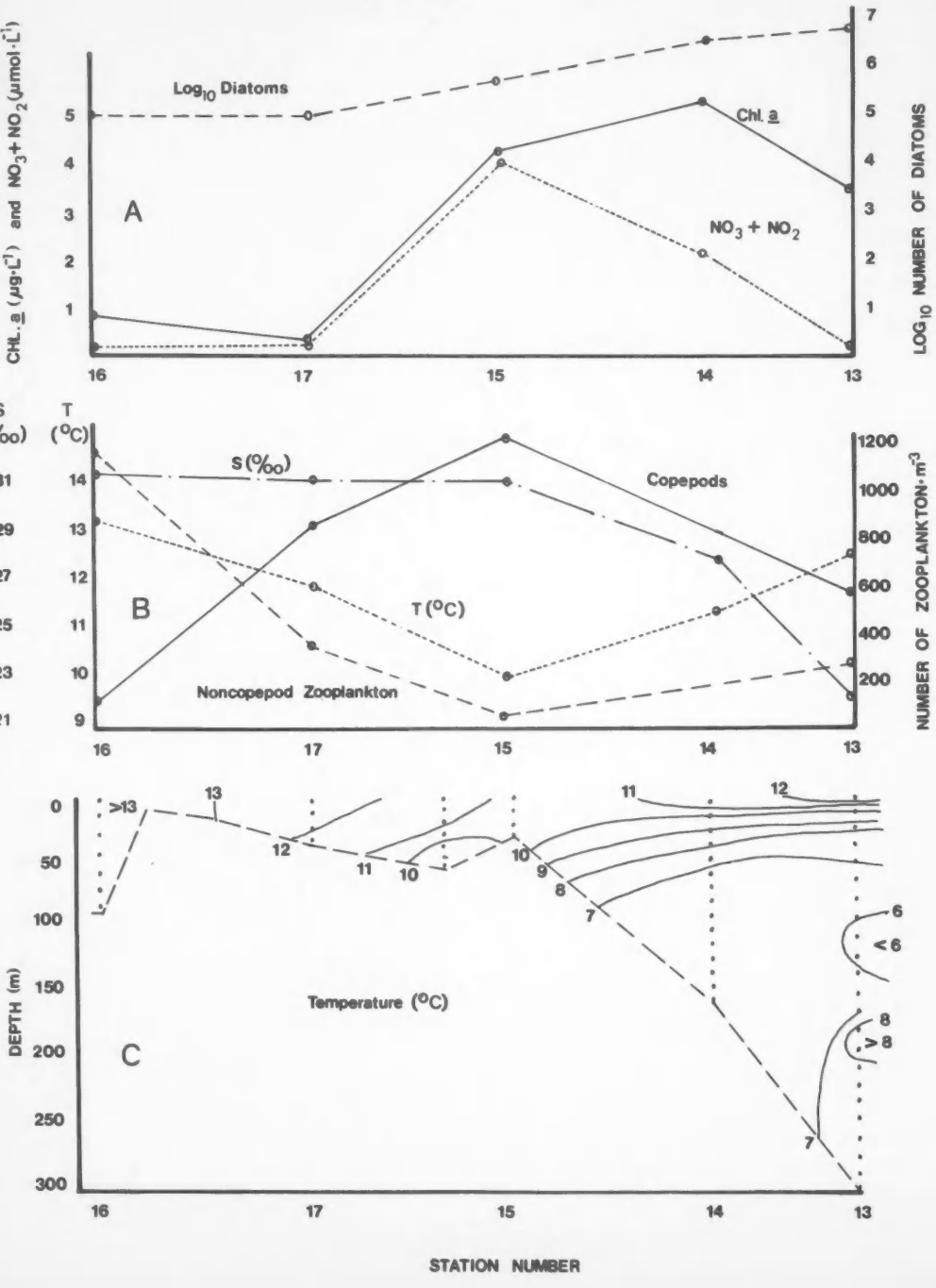


FIG. 5. Station locations. Squares indicate regular sampling stations, triangles represent XBT temperature profiles only. Depth contours in metres. A. Cruise 10, June 27–28, 1979. B. Cruise 11, July 24, 1979. C. Cruise 14, June 2–4, 1980. D. Cruise 15, August 30, 1980. Broken line indicates route of the continuous fluorescence and temperature transect.

where significance represents the probability of the correlation coefficient being equal to zero.

Stations occupied by the *Tofino* on transects across Chatham Sound and northern Hecate Strait are shown in Fig. 5. The same transect was repeated on all three cruises, with occasional stations in Dixon Entrance and off Banks


CHL. a (μg·L⁻¹) and NO3+NO2 (μmol·L⁻¹)
Log10 Diatoms
Chl. a
NO3 + NO2
A
LOG10 NUMBER OF DIATOMS
16
17
15
14
13
S (‰)
T (°C)
S(‰)
Copepods
T(°C)
B
Noncopepod Zooplankton
NUMBER OF ZOOPLANKTON·m⁻³
DEPTH (m)
Temperature (°C)
C
STATION NUMBER

Island in eastern Hecate Strait. Data from the transects are presented in Fig. 6 to 9, with station numbers aligned so they are comparable across all cruises.

Cruise 10 (June 1979) has been divided into two transects, a northern transect from Chatham Sound to Sandspit, Queen Charlotte Islands (Fig. 6), and a central transect from Sandspit back to Prince Rupert at the mouth of the Skeena River (Fig. 7). On the northern transect (Fig. 6), concentrations of chlorophyll, diatoms, nitrate, and copepods were lowest in the well-mixed, shallow western strait (Fig. 6C), and higher in the stratified eastern strait. The sharpest change occurred where vertical stratification appeared and surface temperature was a minimum (station 15). The decrease of salinity at the easternmost stations represents the effect of the Skeena and Nass rivers in Chatham Sound.

Compositional differences of phytoplankton occurred to the east and west of station 15. Diatoms were less than 10% (as numbers) of the total population of phytoplankton on the shallow shelf (stations 16 and 17), whereas in deeper water at stations 15, 14, and 13 they comprised 31, 57, and 81%, respectively. Table 1 presents proportional similarity indices for cruises 10 and 11 calculated according to Kohn and Riggs (1982) using the number$\cdot L^{-1}$ of centric and pennate diatoms at each station. The panel for cruise 10 (northern transect) indicates the stations can be separated into two groups, stations 16 and 17 in the western mixed region, and 15, 14, and 13 in the stratified region. The most common diatom taxonomic group at all stations on the transect was *Skeletonema costatum* (<10-μm diameter).

The central transect of cruise 10 (Fig. 7) resembled the northern transect. Maximum concentrations of chlorophyll and diatoms occurred in the stratified waters of central Hecate Strait adjacent to the western mixed region. The numerically dominant phytoplankton group was again *S. costatum*, although the composition of diatoms varied along the transect (low proportional similarity between stations 16 and 19, see Table 1). The influence of the Skeena River was apparent at the eastern end of the transect from low salinity and high nitrate concentrations.

In July 1979 (cruise 11, Fig. 8), diatom and chlorophyll concentrations were lower than the previous month. Nitrate remained low throughout the surface waters of Hecate Strait, except in Chatham Sound near the Skeena River. A strong thermal front ccurred at the edge of the western shelf (Fig. 8C) assuming the western strait to be well mixed as indicated by the other vertical temperature diagrams. Diatoms comprised 26% of the total number of phytoplankton at station 15, 39% in the Skeena River outflow (station 13), and 10% at all other stations. Stations 14 and 15 in central and east Hecate Strait were most similar in terms of their diatom composition, whereas stations 17 and 13, at opposite ends of the transect, were least similar (Table 1).

Data from early June 1980 (cruise 14, Fig. 9) shows chlorophyll and copepods were high in eastern Hecate Strait, although peak concentrations did not occur at the same station. The numerically dominant copepods in Hecate Strait were the same on this cruise as during cruise 10 in June 1979. *Acartia longiremus* and *Centropages mcmurrichi/abdominalis* (not separated to species) comprised over 90% of the total number of copepods identified from the stations near the frontal region on these two cruises (data in Perry et al. 1981). Noncopepod zooplankton were not abundant except in June 1979 (cruise 10) and 1980 (cruise 14) near the Queen Charlotte Islands. In 1979 decapod larvae dominated at over 1100 individuals$\cdot m^{-3}$ (97% of the total noncopepod zooplankton) whereas in 1980 brachyuran zoea were most abundant (98% by number). Brachyuran zoea were still a significant component of the noncopopod zooplankton (35% by number) at station 19 on the edge of the western shelf in 1980.

Figure 10 presents the continuous horizontal transect of chlorophyll fluorescence, temperature, and approximate bathymetry across central Hecate Strait for cruise 15 (August 1980). Chlorophyll fluorescence was roughly inversely related to bathymetry and surface temperature, being low over the western shelf and high to the east. The vertical temperature profile shows the increase in fluorescence coincident with the onset of vertical stratification. Note the two major peaks of fluorescence appear to correspond to slightly warmer surface temperatures and increases in the depth of the bottom. A continuous transect of chlorophyll fluorescence in June 1980, following the same route, showed a similar pattern. Fluorescence was low over the western shelf, increased to a peak at the western edge of the deep trough, then dropped sharply and remained low to the east of the trough.

The problem of smearing and the inability to resolve small spatial features in horizontal transects using a sea chest intake system have been avoided in the presentation of these transects. Typical ship's speed was about 20 km$\cdot h^{-1}$ (10 knots), and with a digitizing interval of 3 min this represents a spatial digitizing interval of 0.9 km (0.5 nm), within the resolution of such a system.

Discussion

Data collected from Hecate Strait in 1979 and 1980 are consistent with the locations of mixed and stratified water masses predicted by the Simpson–Hunter stratification parameter (Fig. 3). Vertical temperature profiles indicate mixed conditions over the shallow western strait and stratified conditions to the east. Chlorophyll concentrations and diatom numbers are lowest in the mixed water, higher in the stratified water, but highest in the central strait with the onset of vertical stratification. This is the transition zone and would be expected to have the highest phytoplankton biomass according to the tidal front model. Continuous transects of near-surface fluorescence in June and August 1980 show sharp changes of fluorescence and temperature across Hecate Strait which are likely to indicate precise locations of fronts within this transition zone.

FIG. 6. Data from Cruise 10, northern transect from Chatham Sound to Sandspit, June 27, 1979. A. Near-surface (3 m) chlorophyll *a* (μg$\cdot L^{-1}$), $NO_3 + NO_2$ (μmol$\cdot L^{-1}$), diatoms ($\log_{10}$ Number$\cdot L^{-1}$). B. Near-surface copepods, other zooplankton (noncopepod zooplankton), salinity, and temperature. C. Vertical dots represent XBT temperature profiles; bottom topography is approximated from these profiles.

TABLE 1. Proportional similarity of stations based on their centric and pennate diatom composition using the sample-size independent index of Kohn and Riggs (1982): $PS_i = 1 - 0.5 \sum_{i=1}^{s} |P_{x,i} - P_{y,i}|$ where $P_{x,i}$ is the proportion of taxonomic group i in sample x, similarly with $P_{y,i}$ for sample y, and S is the total number of taxonomic categories.

Cruise 10 (north) — diatoms

Stn	17	15	14	13
16	0.59	0.46	0.45	0.51
17		0.48	0.54	0.45
15			0.73	0.86
14				0.81

Cruise 10 (central) — diatoms

Stn	17	18	19
16	0.59	0.46	0.23
17		0.56	0.40
18			0.34

Cruise 11 — diatoms

Stn	16	15	14	13
17	0.38	0.30	0.29	0.09
16		0.47	0.41	0.05
15			0.69	0.34
14				0.34

Zooplankton parallel the pattern for phytoplankton, except for the large numbers of decapod and crab larvae sampled in June near the Queen Charlotte Islands. These may be remnants of the spring bloom which presumably had dispersed or settled to the bottom by midsummer. In this region, crab larvae are known to become free swimming during April, with the larval stage lasting about 4 mo (Butler 1956).

The correspondence of field data with predicted mixing characteristics occurs even without considering the effects of freshwater input. The front model assumes the surface buoyancy flux is due solely to surface heating, but freshwater also increases the buoyancy of the surface layer and reduces the effect of bottom mixing. Hecate Strait is influenced by freshwater in summer, especially from the Skeena River in the north and to a lesser extent along the mainland shore to the east. Applicability of the tidal front model to areas where salinity effects occur has already been noted for Hudson Bay (Griffiths et al. 1981) and the Gulf of St. Lawrence (Iles and Sinclair 1982), although the latter authors do comment the parameter may indicate relative degrees of mixing rather than precise locations of fronts.

However, there are two important aspects of the data which are not consistent with the shallow sea tidal front model as outlined for the British Isles. Near-surface temperatures are consistently higher on the well-mixed western shelf than in eastern Hecate Strait, often with a minimum in central Hecate Strait at the stations in the frontal zone, and nitrate plus nitrite concentrations on the western mixed side are anomalously low for a typical tidal front (see Pingree 1978; Pingree et al. 1978).

The simplest explanation for these discrepancies is the very shallow depth of western Hecate Strait. Most of this region is considerably less than 30 m, and well mixed from surface to bottom according to the vertical temperature profiles. Tabata (1958), in a study of the annual heat budget about Triple Island in eastern Dixon Entrance, has estimated that heat gained by the sea in summer would be able to raise the temperature of a 50-m water column by 0.8°C per month if advective effects were neglected. In western Hecate Strait, this amounts to continually heating the whole water column, whereas eastern Hecate Strait would experience mixing of cooler deeper water into the stratified layer with the passage of occasional storms.

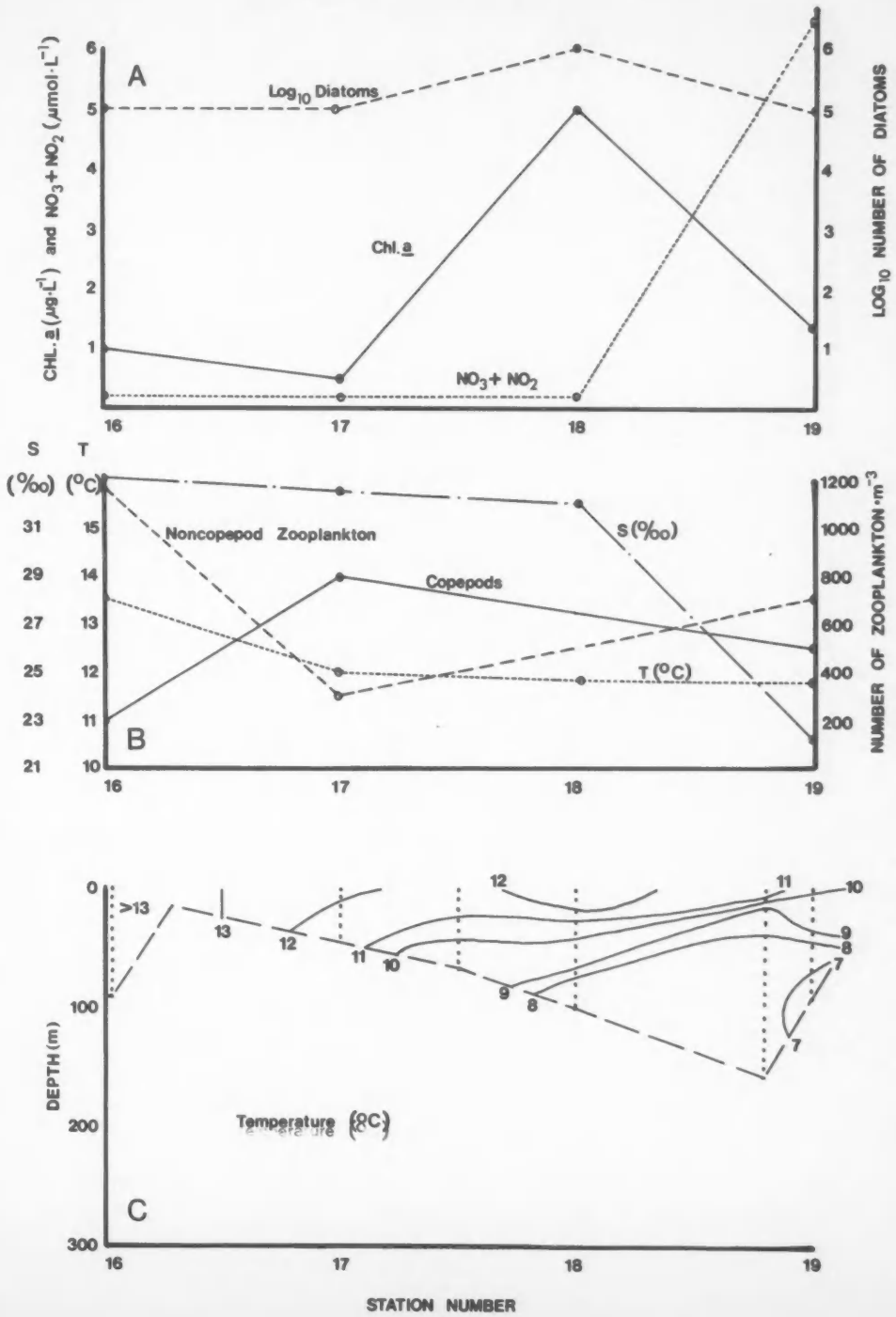
Low nutrient concentrations in western Hecate Strait result if the region has low nutrients all year or becomes depleted before summer and remains so until later in the year. Data in Dilke et al. (1979) and Perry et al. (1981) show high nitrate plus nitrite concentrations in western Hecate Strait in winter (January 1979, February 1980), between 10 and 20 μmol $NO_3 \cdot L^{-1}$, that decreases to less than 3 μmol $NO_3 \cdot L^{-1}$ during the spring bloom. We suggest that nitrate concentrations are then kept low in summer by continual but low, probably nutrient-limited, phytoplankton growth. This is consistent with the observation that in very shallow environments, high mixing may not lead to light limitation of phytoplankton (Legendre 1981).

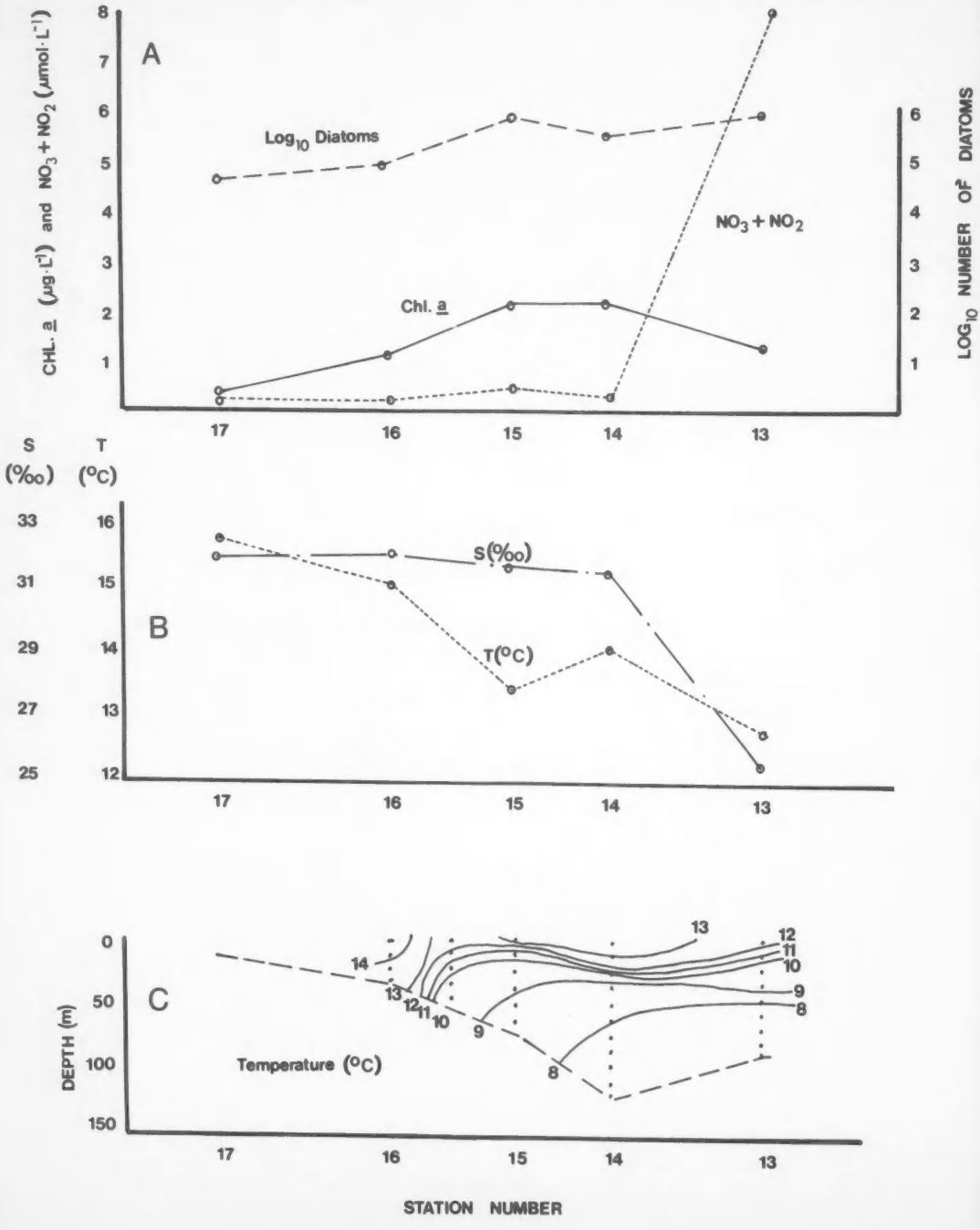
To determine if western Hecate Strait is indeed shallow enough to prevent light limitation of phytoplankton, we calculated the critical depth for June using the equation in Parsons et al. (1977a, p. 99). The monthly radiation (I_0 = 1784 $J \cdot cm^{-2} \cdot d^{-1}$) is the normal incident radiation for June at Sandspit on the Queen Charlotte Islands as published in the Monthly Radiation Summary of Environment Canada (Anon. 1980). This was corrected for surface reflection due to sun angle (0.96 from Parsons et al. 1966). The attenuation coefficient k was determined as the mean of $1.45/Z_s$ (Walker 1980), where Z_s was the secchi disk depth measured in western Hecate Strait during June (seven measurements: Strickland 1958; P.O.G. 1959, 1962).

The compensation light intensity I_c was chosen as 58 $J \cdot cm^{-2} \cdot d^{-1}$ from work by Hobson (1981) on phytoplankton in Saanich Inlet, B.C. This value is at the high end of the range of compensation intensities determined for *S. costatum* by Falkowski and Owens (1978) but well within the full range of intensities given for the six species of marine phytoplankton tested in their study. Using a mean attenuation coefficient of $0.178 \cdot m^{-1}$ the calculated critical depth for western Hecate Strait in June is 83 m, with a standard deviation of 34 m based on variation in the secchi depth measurements. Data for July indicate similar critical depths. This is considerably deeper than the depth of the western shelf and suggests phytoplankton will not be light limited in this region.

Tidal mixing therefore appears to be a plausible mechanism generating mixed conditions over the shallow western regions of the strait, and stratified conditions on the eastern side. Phytoplankton concentrations are low in summer in both these areas as a result of nutrient limitation. However, nutrients may be mixed sporadically into the surface waters of the

FIG. 7. Cruise 10, central transect from Sandspit to Prince Rupert, June 28, 1979. Details of A, B, C as for Fig. 6.


A
Log10 Diatoms
Chl. a
NO3+ NO2
CHL. a (μg·L-1) and NO3+ NO2 (μmol·L-1)
LOG10 NUMBER OF DIATOMS
S (‰)
T (°C)
B
Noncopepod Zooplankton
Copepods
NUMBER OF ZOOPLANKTON·m-3
C
DEPTH (m)
Temperature (°C)
STATION NUMBER


A
CHL. a (μg·L⁻¹) and NO3 + NO2 (μmol·L⁻¹)
LOG10 NUMBER OF DIATOMS
Log10 Diatoms
NO3 + NO2
Chl. a
B
S (‰)
T (°C)
S(‰)
T(°C)
C
DEPTH (m)
Temperature (°C)
STATION NUMBER
17
16
15
14
13

stratified region with the passage of local storms. For example, the depth of the wind-mixed (Ekman) surface layer can be estimated from the equation (Pond and Pickard 1978, p. 88)

$$D_E = \frac{4.3\ W}{\sqrt{\sin \phi}}$$

where D_E is the Ekman depth, W the wind speed, and ϕ the latitude. Using a maximum hourly wind speed of 12 $m \cdot s^{-1}$ recorded from Sandspit and McInnes Island on opposite sides of Hecate Strait on August 22, 1980 (Atmospheric Environment Service 1980), the calculated wind-mixed layer was ~58 m. Such vertical mixing may account for the higher near-surface fluorescence of eastern Hecate Strait apparent in Fig. 10. Considering the mixed side has low nutrient concentrations, where do the nutrients come from to sustain high plankton biomass in the frontal region of central Hecate Strait?

One possibility is the existence of a front between northern Hecate Strait and Dixon Entrance parallel to the rather steep bathymetry. Little nutrient data are available from this area, although three stations north of Graham Island in July 1979 indicate nitrate plus nitrite concentrations greater than 1–2 μmol $NO_3 \cdot L^{-1}$ (data in Perry et al. 1981), whereas concentrations in Hecate Strait itself were less than 0.5 μmol $NO_3 \cdot L^{-1}$ (Fig. 8). The transect from Sandspit through eastern Dixon Entrance to Chatham Sound (Fig. 6) shows anomalously high nitrate at station 15 near Rose Spit, is in the area frontal activity might be expected.

A second possible source of nutrients to central Hecate Strait surface waters is episodic upwelling along the rapid change of bathymetry from the eastern trough to the western shelf. Such a mechanism has been proposed to account for the high productivity of a front off Nova Scotia (Fournier et al. 1977), where nutrient-rich slope water is advected onto the shelf at the shelf break. H. Sandstrom and J. A. Elliot (Atlantic Oceanographic Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S., 1982) have estimated that mixing by solitary waves of the internal tide at the shelf break is sufficient to supply the required nutrient flux calculated by Fournier et al. (1977). Sandstrom and Elliot further suggest such interactions of the internal tide with shelf topography are likely to occur at other sites along continental shelves and banks. Denman et al. (1981) describe zones of high phytoplankton biomass and productivity on the continental shelf off the west coast of Vancouver Island. They suggest these zones result from advection of nutrient-rich deep water onto the shelf due to the interaction of alongshore currents, including the California Undercurrent, with the complicated bathymetry of the area. Such a mechanism, or some interaction of internal tides at the edge of the continental shelf in Queen Charlotte Sound, may cause movement of nutrient-rich deep water into the surface layer of central Hecate Strait. That Pacific Equatorial Water does occur in Hecate Strait was indicated by Gardner (1982b) from temperature and salinity characteristics and the occurrence of normally subtropical zooplankton species in 1977.

Barber (1957) has suggested light northwest winds during summer can produce slight upwelling along the mainland shore of Hecate Strait, due to both offshore Ekman transport and the rebound of isopycnals depressed during strong winter southeast winds. The greatest effect of such upwelling would be expected in eastern Hecate Strait. Data presented in this study, however, do not indicate an effect of such upwelling on upper-layer plankton biomass. The spatial scale of discrete sampling stations may have been too coarse to detect such an effect, although near-surface fluorescence measured continuously across the strait was also low near the eastern shore (Fig. 10).

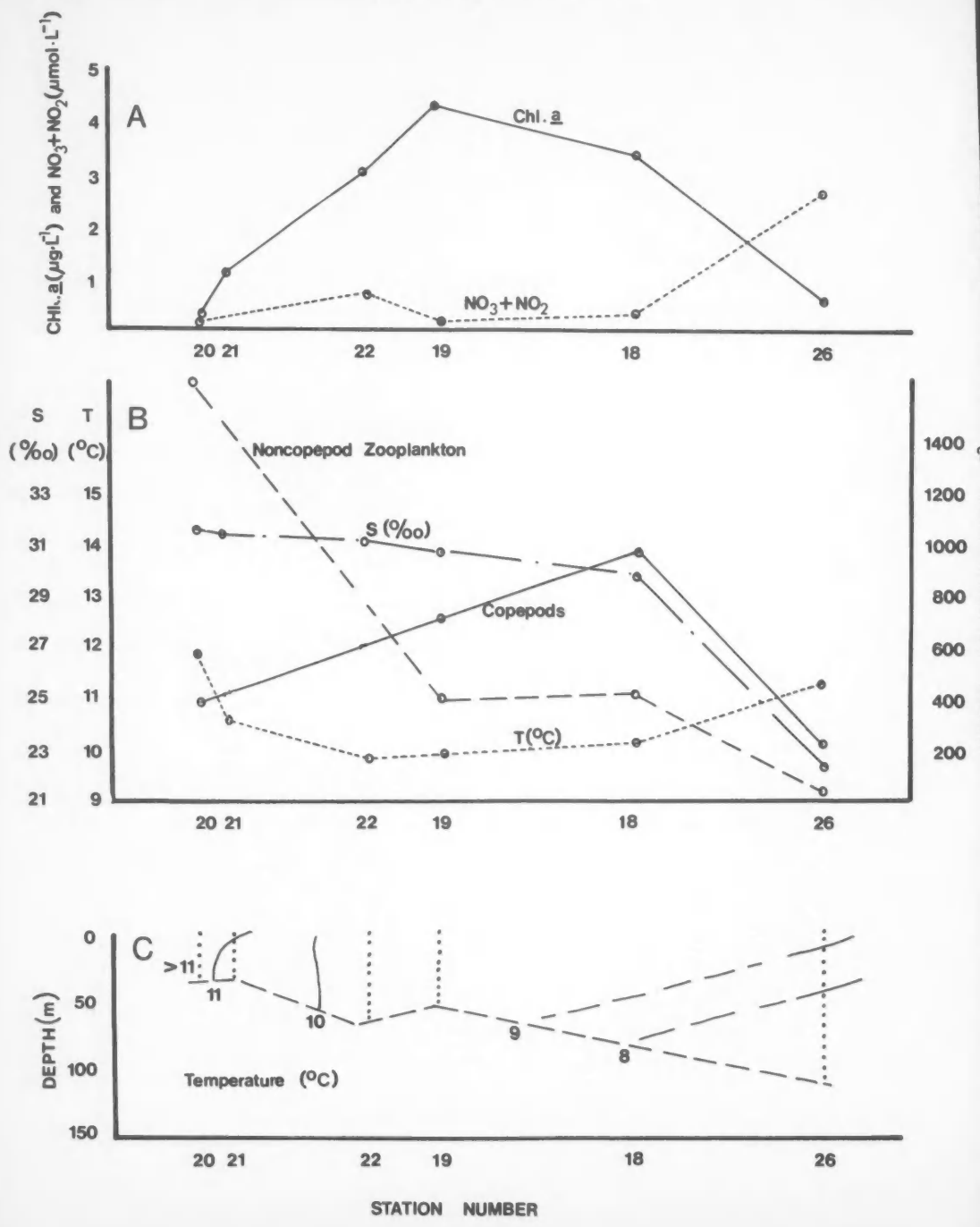
It is interesting to speculate on the effects a frontal system in central Hecate Strait might have on fish production. Considering the depth of western Hecate Strait it is reasonable to expect substantial exchange of upper-layer primary production with the benthos. The amount of production which will sediment to the bottom depends on the depth of the bottom, the depth of mixing, and the amount of primary production or biomass. More material sediments to the bottom in shallow rather than deep environments (Mills 1980), under shallow mixed layer depths (Hargrave 1973), and when upper-layer primary production is high (Parsons et al. 1977b). In western Hecate Strait, considerable biomass could be expected to sediment to the benthos because of the depth of the water. However, during summer our data show phytoplankton biomass is generally low, and mixing may keep such sedimented material in suspension for some time.

In the frontal region at the shelf break, the above three criteria appear to be optimal. The depth of the bottom is relatively shallow, although as the bathymetry changes rapidly in the east–west direction, this depends on the location of the front. Mixed layer depths are shallower than over the western shelf, reflecting the onset of vertical stratification, and phytoplankton biomass is relatively high, all suggesting the possibility of considerable transfer of material to the benthic layer.

Given such a scenario, it is perhaps not surprising to find Hecate Strait is the most productive groundfish region of the B.C. coast, with Pacific cod (*Gadus macrocephalus*) the greatest proportion of the catch. Of all Pacific cod landed from Hecate Strait between 1958 and 1978, 83% were caught along the edge of the western shelf at approximately the 40-m isobath, and at similar depths between Hecate Strait and Dixon Entrance (Stocker 1981). Very little is known of pelagic fish production and distributions in Hecate Strait, except that extensive herring and salmonid migrations occur at certain times of the year. Studies of other systems have generally found that fish associate closely with fronts, probably through feeding (Owen 1981).

A potential energy budget for a system similar to that described here, involving shallow depths, tide and wind mixing, and deepwater nutrient supply, has been outlined by Cohen et al. (1982) for Georges Bank. They found that high primary production throughout the summer was able to sustain both high pelagic fish production and high demersal fish production via a pathway through the macro- and meio-benthos.

FIG. 8. Cruise 11, July 24, 1979. Details of A, B, C as for Fig. 6.


A
Chl. a
NO_3+NO_2
Chl. a (μg·L⁻¹) and NO_3+NO_2 (μmol·L⁻¹)
B
Noncopepod Zooplankton
S (‰)
Copepods
T(°C)
S (‰)
T (°C)
NUMBER OF ZOOPLANKTON m⁻³
C
>11
11
10
9
8
Temperature (°C)
DEPTH (m)
20 21 22 19 18 26
STATION NUMBER

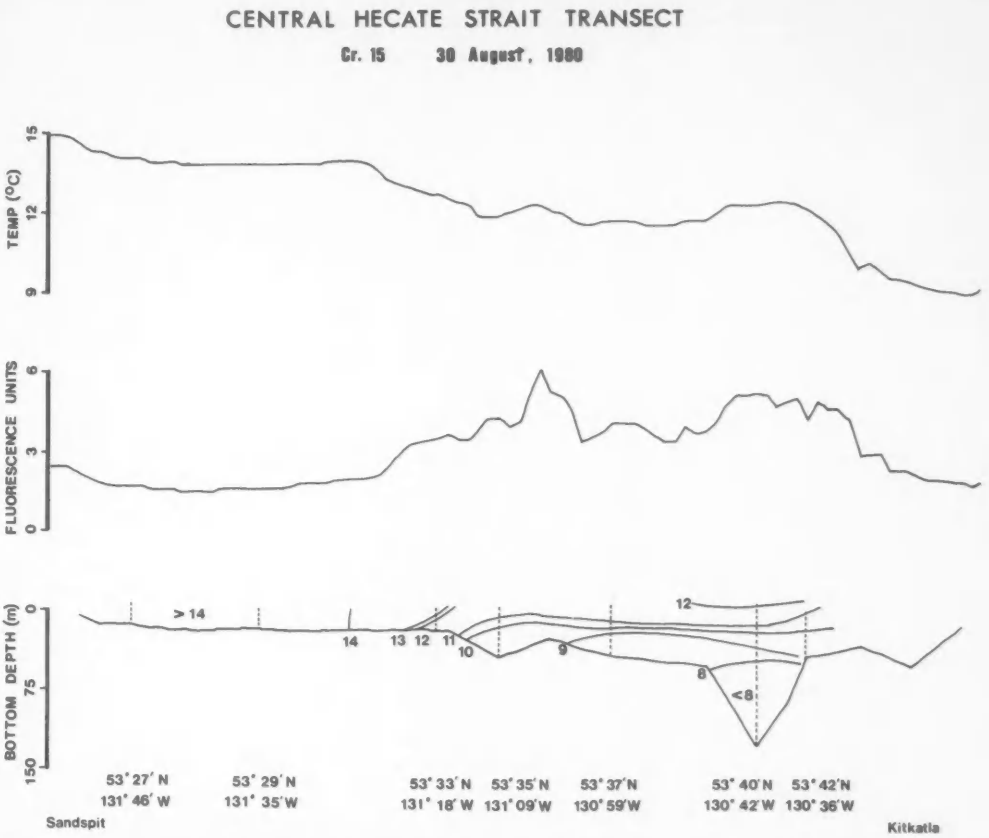


FIG. 10. Cruise 15, August 30, 1980. Continuous transect from Sandspit, Queen Charlotte Islands, to Kitkatla. Note this is not the same transect as Fig. 6 to 9. Top: near-surface (3 m) temperature. Middle: near-surface relative fluorescence. Bottom: vertical temperature structure (°C) derived from XBT profiles (vertical dots) and the approximate bottom topography.

Little is known of the productivity or biomass of benthic organisms in central Hecate Strait, and whether they might form a link between high plankton biomass at the front and high groundfish production.

In summary, we have presented the first data available concerning tidal mixing effects and plankton distributions in Hecate Strait. We identified areas important to plankton production and suggested how these might relate to higher trophic levels. More detailed information on distributions and rates of energy exchange are needed to begin to identify critical areas for the production and survival of commercial marine resources in this region.

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FIG. 9. Cruise 14, June 2–4, 1980. Details of A, B, C as for Fig. 6.

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Nocturnal Inshore Movement of the Mimic Shiner (*Notropis volucellus*): a Possible Predator Avoidance Behavior

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Diel seining documented a significant summer nocturnal inshore movement of the mimic shiner (*Notropis volucellus*) in Lake Itasca, Minnesota. This species initiated inshore movement at sunset, occupied the nearshore area throughout the night, and moved offshore by sunrise. Mimic shiners were collected in less than 1 m of water throughout inshore areas with sparsely developed macroscopic vegetation. Greatest relative abundance was observed at sites possessing the greatest expanse of sparsely or nonvegetated substrate. Relative abundance at inshore sites may be related to habitat characteristics of the sites or to the proximity of feeding habitat. These diel movements differed markedly from those exhibited by the mimic shiner in other lakes. The inshore movement in Lake Itasca may function to reduce crepuscular and nocturnal predation pressure. Our data support the hypothesis that freshwater fishes may possess behavioral plasticity sufficient to alter movement and distribution patterns according to prevailing conditions and that predation pressure may be important in altering prey behavioral patterns.

HANYCH, D. A., M. R. ROSS, R. E. MAGNIEN, AND A. L. SUGGARS. 1983. Nocturnal inshore movement of the mimic shiner (*Notropis volucellus*): a possible predator avoidance behavior. Can. J. Fish. Aquat. Sci. 40: 888–894.

Des pêches nycthémérales à la senne démontrent un mouvement nocturne significatif en été du méné pâle (*Notropis volucellus*) vers le rivage, dans le lac Itasca, au Minnesota. Cette espèce se dirige vers le rivage au soleil couchant, se tient près du bord toute la nuit et retourne au large au soleil levant. On a capturé des ménés pâles à des profondeurs inférieures à 1 m dans toutes les régions côtières à végétation macroscopique éparpillée; le maximum d'abondance relative se trouve à des sites possédant la plus grande étendue de substrat avec peu ou pas de végétation. Aux sites côtiers, il se peut que l'abondance relative soit reliée aux caractéristiques d'habitat ou à la proximité des aires d'alimentation. Ces mouvements nycthéméraux diffèrent nettement de ceux qui ont été observés chez les ménés pâles d'autres lacs. Des signes indirects nous font croire que le mouvement vers la rive a pour function d'atténuer la pression d'une prédation crépusculaire ou nocturne. Nos données appuient l'hypothèse que les poissons d'eau douce ont un comportement suffisamment flexible pour modifier leurs habitudes migratoires et leur distribution selon les conditions et que la pression de prédation peut jouer un rôle important par modification du comportement des proies.

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DIEL migrations have been reported for numerous fish taxa. Studies have described vertical movements associated with diel distribution patterns of zooplankton food (Narver 1970; Begg 1976; Eggers 1978; Zaret 1980), horizontal movements to and from coral reefs for resting and feeding (Smith and Tyler 1972; Collette and Talbot 1972; Hobson 1972, 1973; Domm and Domm 1973), and inshore–offshore movements of freshwater lentic species (Black 1945; Hasler and Bardach 1949; Emery 1973; Moyle 1973; Baumann and Kitchell 1974; Keast et al. 1978; Hall et al. 1979; Bohl 1980; Helfman 1979, 1981). Although diel migrations are conducted by numerous marine fishes in coral reef systems, diel inshore–offshore movements in freshwater lakes appear to be characteristic of relatively fewer species (Emery 1973; Keast et al. 1978; Helfman 1981). Helfman (1981) suggested that freshwater fishes, due to the great variability of biological and environmental parameters within and among freshwater ecosystems, may have evolved behavioral plasticity sufficient to alter daily movements according to prevailing conditions. However, little information is available suggesting that freshwater species exhibit different daily movement patterns among lakes.

In this paper we describe diel nocturnal inshore movements of the mimic shiner (*Notropis volucellus*) in Lake Itasca, Minnesota, that differ markedly from those described for the same species in other lakes and discuss the potential relationship between the density and composition of predator assemblages and the types of diel movements exhibited by the mimic shiner in particular lake systems.

Study Sites

Lake Itasca is a 436-ha natural lake situated at the headwaters of the Mississippi River in Clearwater County, north-central Minnesota. It is a eutrophic lake (Cole and Underhill 1965) with extensive growths of emergent and submergent rooted aquatic vegetation. Maximum depth and mean depth are 14 m and 5.2 m, respectively. Over 50% of the lake is littoral (Cole and Underhill 1965). During the summer Lake Itasca stratifies at about 6.0 m, with the hypolimnion becoming anoxic or nearly so. The fish community has abundant predators, with northern pike (*Esox lucius*), walleye (*Stizostedion vitreum*), largemouth bass (*Micropterus salmoides*), black crappie (*Pomoxis nigromaculatus*), yellow perch (*Perca flavescens*), rock bass (*Ambloplites rupestris*), and brown bullhead (*Ictalurus nebulosus*) having self-sustaining populations.

Study sites were sparsely or nonvegetated shoreline areas bordered laterally by growths of emergent and submergent aquatic vegetation. Site A was adjacent to the University of Minnesota's Lake Itasca Forestry and Biological Station (Fig. 1). The 35-m-wide sparsely vegetated area was bordered laterally by dense emergent *Potamogeton natans*, *Scirpus acutus*, *Zizania aquatica*, *Nuphar variegatum*, and *Nymphaea odorata* and by submergent *Potamogeton* spp. The substrate in the open area was composed of gravel, silt, and rocks with small scattered patches of submergent *Chara* sp., *Anacharis canadensis*, and *Potamogeton* spp. Site B consisted of a 160-m-wide open area with sand and silt substrate. Submergent growths of *Chara* sp., *Najas flexilis*, *Heterantha dubia*, and *Ceratophyllum demersum* were sparsely scattered within the open area, with more extensive growths beginning approximately 40–50 m offshore. The site was bordered laterally by small patches of *Zizania aquatica*, *Scirpus* sp., and *Phragmites australis*. Site C possessed gravel and silt substratum moderately covered by patches of *Chara* sp. and *Potamogeton* spp. with more extensive patches of *Chara* sp. beginning 20 m offshore. Bordering the 65-m-wide open area were growths of *Scirpus* sp., *Zizania aquatica*, *Nuphar variegatum*, and *Nymphaea odorata*.

Water depths at 10–15 m from the shoreline were 0.8–1.1 m at the sites, with depths of approximately 1.5 m (sites A and C) and 3 m (site B) at 50 m from shore.

Methods

Collections were made during the summers of 1981 and 1982. Seine hauls were made every 3 h for a 24-h period once at each site and over several periods bracketing sunset at the sites. In addition, hourly samples were collected from 18:30 to 21:30 at site B and from 03:30 to 06:30 at site A. One hour before a sampling series was initiated, the area to be sampled was delimited by driving stakes into the lake substrate 15 m apart and approximately 15 m from shore at sites A and C and 16 m from shore at site B. Water depth at the stakes was 0.8–1.1 m. The seine used in all sampling was 1.3 × 5.0 m with 0.4-cm mesh. The mesh size was small enough to prevent all but young-of-the-year fishes from passing through the netting. Sampling at each time period consisted of three seine hauls from the outer boundary of the sampling area to the shore. The first haul was started at one side of the delimited area, the second at the other side, and the third midway between the stakes. Thus, an area of 225 m^2 was seined at sites A and C and 240 m^2 at site B. We always approached the starting point from outside the marked area, so the water to be sampled was undisturbed immediately before seining. All cyprinids were preserved in 10% formalin for later identification, except for samples taken at site A on 11–12 July and 11 August 1981 where fishes were identified, counted, and returned to the water alive.

An entrapment technique was used to determine whether net avoidance prevented capture of cyprinids during the day. In this procedure, 12-m seines were drawn shoreward perpendicular to the shoreline from each end of the collecting seine. This required approximately 10 s and resulted in the water to be sampled being entirely enclosed. The sampling seine and a following seine of the same size were then pulled to shore through the entrapped area and all captured cyprinids were preserved. A similar technique was shown to have high capture efficiency by Conover and Ross (1982). This procedure was conducted during one midafternoon (15:30) and one post-sunset (21:30) collecting period at site B.

One nighttime and 12 daytime transects were snorkeled to aid in verifying the seining data. Daytime transects, 20 m in length and oriented parallel to shore, were swum at 10 m (depth 0.5–0.7 m) and 30 m (depth approximately 1.5 m) from shore. Four transects at each distance were located in open water areas and two transects at each distance were in the emergent and submergent vegetation adjacent to the sampling areas. Day transects were divided among the sampling sites, while the single night transect was conducted at site B at

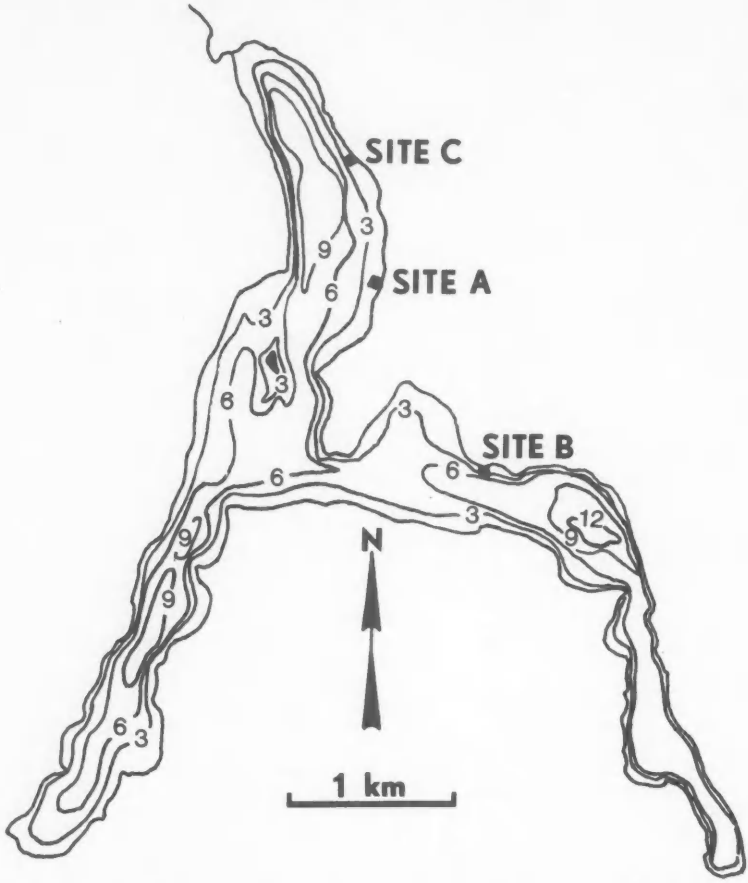

FIG. 1. Study sites and depth contour intervals (metres) for Lake Itasca, Itasca State Park, Clearwater County, Minnesota.

22:00, approximately 1.5 h after sunset. This night transect was located 10 m from shore in 0.7 m of water.

Since mimic shiners have been reported to feed diurnally in shallow inshore areas and rest farther offshore nocturnally (Moyle 1973), we conducted a gut fullness analysis to determine their pattern of feeding while distributed inshore nocturnally in Lake Itasca. Samples of mimic shiners were collected and preserved at 21:30, 00:30, and 03:30 at site B. Each fish was placed in an individual preservation vial containing 10% formalin, which allowed subsequent analysis of food materials regurgitated into the formalin as well as material retained in the gut. We recorded the general degree of fullness of fore- and mid-sections of the digestive tract. After dissection these sections were categorized as empty, full, or housing material but less than full. A full tract was defined as having the entire length of the section examined filled with material; no attempt was made to quantify the degree of distension of the gut. The solution from the vial housing each fish was surveyed at 20× magnification for a 3-min period. Any crustacean zooplankters, aquatic insects, or identifiable parts of these organisms were considered to have been regurgitated food. One investigator categorized each vial as having few items (<2 identified), commonly occurring items (2−10 identified), or numerous items (>10).

Results

The occurrence of cyprinids in open inshore areas increased dramatically after sunset (Table 1). Significantly greater numbers of cyprinids were captured during the night than day for the three sampling dates that encompassed a complete 24-h period ($P < 0.05$, Mann−Whitney U-test, Table 1). Hourly

TABLE 1. Numbers of mimic shiners and total cyprinids captured in three seine hauls per sampling period at the study sites. Other taxa comprising a substantial proportion of total cyprinids captured per sampling date are included. Sunrise occurred prior to 06:30 and sunset prior to 21:30.

Site	Date	Taxon	06:30	09:30	12:30	15:30	18:30	21:30	00:30	03:30
A	8–9 July 1981	*N. volucellus*	0	0	0	0	0	0	1	2
		P. notatus	2	1	2	2	4	84	33	31
		Total cyprinids	2	2	2	2	4	88	36	34
A	11–12 July 1981	*N. volucellus*				0	0	1	3	
		P. notatus				1	2	71	29	
		Total cyprinids				1	2	77	39	
A	8–9 July 1982	*N. volucellus*[a]					0	9	3	
		N. cornutus					0	9	1	
		Total cyprinids					9	23	6	
A	11–12 July 1982	*N. volucellus*[a]				0	0	12	14	
		P. notatus				0	0	10	2	
		Total cyprinids				0	0	29	28	
A	27–28 July 1982	*N. volucellus*[a]					0	109	18	
		N. cornutus					2	34	5	
		P. notatus					3	60	7	
		Total cyprinids					5	219	34	
B	12–13 July 1981	*N. volucellus*[a]	0	0	18	0	0	465	147	227
		Total cyprinids	0	0	31	12	9	563	208	279
B	13–14 Aug. 1981	*N. volucellus*[a]					0	1803	631	749
		Total cyprinids					0	1812	641	756
B	30–31 July 1982	*N. volucellus*[a]					0	8450	2634	
		Total cyprinids					57	8570	2703	
C	2–3 Aug. 1981	*N. volucellus*[a]	0	0	0	0	0	60	22	30
		N. cornutus	0	2	1	2	1	53	16	5
		P. notatus	0	0	0	0	0	67	19	10
		Total cyprinids	0	2	1	2	1	180	57	45
C	14–15 Aug. 1981	*N. volucellus*[a]				0	0	106	57	
		Total cyprinids				0	0	153	83	
C	6–7 Aug. 1982	*N. volucellus*[a]					0	807	554	
		Total cyprinids					4	851	591	

[a]Observed distribution of mimic shiners deviated significantly from a uniform distribution ($P < 0.01$, Chi-square analysis).

sampling indicated that the movement to sparsely vegetated inshore areas occurred within the hour bracketing sunset (Table 2). The numbers of cyprinids in site A declined from 03:30 to 06:30 with movement from the area completed by the postsunrise 06:30 sampling period (Table 2). Such movement was not exhibited during hourly sampling between 03:30 and 06:30 on 7 August 1981. This might have been attributable to strong wave action present on that day following 2 d of stormy conditions.

The mimic shiner was the most abundant cyprinid in all night collections made at site B and in all but one night collection (21:30 on 2 August 1981) made at site C (Table 1). However, at site A this species was the most numerous cyprinid only during the night samples of 27–28 July 1982 and the 00:30 sample of 12 July 1982. The bluntnose minnow (*Pimephales notatus*) was the most abundant cyprinid

TABLE 2. Numbers of mimic shiners and total cyprinids during hourly sampling that bracketed sunrise (approximately 06:00) and sunset (shortly after 20:30).

Site	Date and time	*N. volucellus*	Total cyprinids
A	11 Aug. 1981		
	03:30	13	32
	04:30	5	22
	05:30	0	15
	06:30	0	0
B	13 Aug. 1981		
	18:30	0	0
	19:30	0	0
	20:30	545	546
	21:30	1803	1812

TABLE 3. Relative fullness of digestive tracts of mimic shiners collected during postsunset collecting periods.

Category and time	No. of fishes with: full tracts	intermediate	empty	total
Foregut[a]				
21:30	8	5	2	15
00:30	2	10	3	15
03:30	1	3	11	15
Midgut				
21:30	9	2	2	13
00:30	7	5	3	15
03:30	3	2	10	15

[a]Fullness is dependent upon time period ($P < 0.05$, G-test of independence).

collected in all other night samples at site A (Table 1). The bluntnose minnow and the common shiner (*Notropis cornutus*) were approximately equally abundant as the mimic shiner in the 21:30 collection at site C on 2 August 1981.

The numbers of mimic shiners collected deviated significantly from being distributed uniformly through time ($P < 0.01$, Chi-square analysis, Table 1) for all sampling dates except 8–9 July and 11–12 July 1981 at site A. For sampling dates in which the inshore occurrence through time deviated significantly from a uniform distribution, the greatest numbers of mimic shiners were collected during the postsunset (21:30) sampling period, with later nighttime samples producing fewer fishes. The reduction in numbers of cyprinids collected after the postsunset period occurred on 11–12 July 1981 when all cyprinids captured were identified and returned immediately to the water instead of being preserved. Thus, the pattern of reduced abundance in sample sites as night progressed was probably not due to depletion caused by preservation of earlier samples. Within either year the greatest numbers of mimic shiners were collected at site B, the most open inshore site, while the least were collected at site A, the site most enclosed by dense surrounding vegetation.

No minnows were sighted at the sampling sites during any daytime snorkeling census along the 20-m transects. Eighty-two adult minnows were counted along the transect surveyed at 22:00 at site B; nearly all appeared to be mimic shiners. Most were resting on the substrate, while a few were swimming slowly in midwater. The number counted was a conservative estimate because of the limited area illuminated by the flashlight.

No minnows were captured during entrapment seining at 15:30, while 101, mostly mimic shiners, were captured at 21:40 (88% captured by the first of the two seines). Approximately equal numbers of noncyprinid fishes were captured during both entrapment seining periods. Transect and entrapment data indicate that the observed capture rates during our normal sampling routine reflected true changes in temporal use of inshore open areas by the mimic shiner.

The degree of fullness of the foregut of mimic shiners was dependent upon sampling time ($P < 0.05$, G-test of independence), with the fishes preserved at the 21:30 collecting period having the fullest foreguts and the 03:30 sample the least full (Table 3). However, there were no significant differences among the degree of fullness indices of the midgut for any of the sampling periods. These data indicate that the fishes were not actively feeding from 21:30 to 03:30 and that food taken in prior to 21:30 had passed to the midgut by 03:30. Differences in gut fullness were not due to differential rates of regurgitation at preservation. There were no significant differences ($P > 0.05$) among the sampling periods in the amount of food material found in preservation vials.

Discussion

Mimic shiners were probably distributed farther from shore during the day than night in Lake Itasca. Mimic shiners did not occur in sparsely vegetated study sites nor in inshore vegetated areas adjacent to study sites during diurnal periods. Occurrence in any other inshore vegetated areas is unlikely because the species is generally described as an open-water schooler and is normally not found within dense vegetation either while active or resting (Black 1945; Moyle 1973; Helfman 1981).

Nocturnal movements of mimic shiners to open inshore areas in our study differed from diel migrations reported for this species in other lakes. Several studies (Black 1945; Moyle 1973; Helfman 1981) indicated that mimic shiners dispersed offshore at night to rest on the substrate after inshore schools broke up at sunset. Helfman (1981) listed this species as schooling in less than 0.2 m of water during the day and resting on barren substrate at night at depths up to 5.0 m. Likewise, Black (1945) reported that mimic shiners schooled in extreme inshore areas during the day, and Moyle (1973) stated that they had feeding peaks in early morning and evening in deeper water than that inhabited at midday.

Nocturnal movements to sparsely vegetated inshore areas might function in facilitating feeding, in providing proper environmental conditions for rest, or in reducing predation pressure imposed upon this forage species. Since the mimic shiner feeds diurnally and rests nocturnally (Moyle 1973; Helfman 1981; this study), feeding does not appear to be a viable explanation for nocturnal movement to inshore areas. Other studies have found that mimic shiners rest in water up to 5.0 m deep (Moyle 1973; Helfman 1981). Extensive areas of Lake Itasca are shallower than the 6.0-m-deep thermocline;

TABLE 4. Mean number of each predator species taken in gill (G) and trap (T) nets in Lake Itasca and Long Lake, Clearwater County, Minnesota (data from unpublished lake survey summaries of the Minnesota Department of Natural Resources). All gill nets were experimental and 80 m in length. Numbers in parentheses indicate total number of net sets. All nets in all surveys were set for one overnight period.

	Lake Itasca 1960		Lake Itasca 1975		Long Lake 1966		Long Lake 1973	
Species	G (12)	T (24)	G (8)	T (20)	G (12)	T (16)	G (4)	T (8)
Rainbow trout (*Salmo gairdneri*)	0	0	0	0	1.42	0	0.50	0
Northern pike	4.25	0.67	11.00	0.50	0.75	0.12	1.25	0
Yellow perch	135.83	2.63	55.75	7.00	7.66	2.56	11.75	5.38
Walleye	5.75	0.58	5.63	0.45	2.50	0	0	0
Largemouth bass	0.08	0.42	0.38	0.95	1.00	0.25	2.75	3.50
Rock bass	0.33	2.08	2.00	2.75	3.42	4.00	4.50	15.38
Black crappie	0.25	0.63	1.50	0.90	0.33	6.50	2.50	5.38
Brown and black bullhead	0	3.92	1.87	3.50	0	0	0	0

thus, the waters are well mixed and oxygenated. It is unlikely that mimic shiners would be forced by abiotic conditions such as oxygen deprivation to move into nonvegetated, very shallow inshore areas in Lake Itasca to find suitable conditions for rest. Indirect evidence suggests that the nocturnal inshore movement may be serving a predator avoidance function.

Predators can control microdistribution of prey in aquatic ecosystems and are often assumed to be the major force responsible for shaping certain prey behavioral patterns (Stein 1979). Records of predator abundance for Lake Itasca and Long Lake, Clearwater Co., Minnesota (the study lake of Moyle 1973), indicate that the walleye, yellow perch, and northern pike are much more abundant in Lake Itasca (Table 4). The northern pike did not occur in Helfman's (1981) study lake nor did the walleye in Black's (1945). The northern pike and yellow perch were not abundant in Black's study lake, nor was the walleye in Helfman's. The genus *Micropterus* was a dominant predator taxon in the other studies whereas it occurred in relatively lesser abundance than most other piscine predators in Lake Itasca (Table 4). Black (1945) concluded that the diurnal inshore movements of mimic shiners in Shriner Lake, Indiana, were a predator avoidance behavior expressed in response to diurnal feeding activity of the abundant largemouth bass (*Micropterus salmoides*) and smallmouth bass (*M. dolomieui*). The mimic shiner showed identical movement in other studies (Moyle 1973; Helfman 1981) in which the genus *Micropterus* constituted a probable major source of piscine predator pressure.

If movement patterns of mimic shiners to extreme inshore areas in Lake Itasca are a predator avoidance behavior, this behavior would appear to be in response to predation pressure that peaked at sunset and continued through the night. The walleye, northern pike, yellow perch, and black crappie, all abundant in Itasca, have been shown to have feeding peaks during crepuscular or nocturnal periods of the day (Lawler 1969; Scott and Crossman 1973; Eddy and Underhill 1974; Casselman 1978). Furthermore, Eddy and Underhill (1974) listed the yellow perch and walleye as important predators of the mimic shiner. The effectiveness of crepuscular and nocturnal predators relies in part on their capacity to strike at backlit prey from below (Hobson 1966; Casselman 1978; Hall et al. 1979). At Lake Itasca the movement at sunset to very shallow inshore areas might be a behavior functioning to reduce the capacity of the abundant crepuscular and nocturnal piscivores to silhouette prey and to move prey away from areas of intense predation. Emery (1973) concluded that crepuscular predators were a selective force affecting the breadth of the temporal aspect of the niche of prey species. Selection should tend to favor behavioral patterns taking the prey species out of areas of intense predation pressure, particularly at dusk when schooling behavior becomes less precise or breaks down and predators feed heavily on "milling prey species" (Emery 1973). In Lake Itasca the decline in inshore abundance during the late night sampling periods may reflect a tendency for the mimic shiner to move farther from the shoreline as the crepuscular predators become less active.

The greater nocturnal abundance of the mimic shiner at sites B and C than at site A may be due to the habitat characteristics of the sites and the adjoining areas. These sites had greater expanses of sparsely vegetated open water with which the mimic shiner is typically associated. Further, the presence of low-lying vegetation forms such as *Chara* offshore from these sites would indicate that potentially good feeding habitat was adjacent to the inshore open areas. The greatest production of food in Lake Itasca for planktivores occurs in areas possessing extensive mats of *Chara* at depths of 0.5−3.0 m (W. Doolittle and M. Whiteside, University of Tennessee, personal communication). In coral reef communities where predation pressure is high, many fishes enter shelter shortly after feeding ceases at dusk, reducing the time period of vulnerability to predation to a minimum (Hobson 1972; Ehrlich et al. 1977). The distance that prey travel between feeding sites and a refuge should be reduced under heavy predation pressure (Covich 1976). Intense crepuscular predation pressure in Itasca could cause selection for a reduction in the amount of time schooling species are exposed to that predation. If movement to extremely shallow water affords resting fishes protection, the utilization of a particular inshore area for resting by a species may be related to its proximity to the area in which the species feeds. The inshore distribution of the bluntnose minnow in Lake Itasca supports this hypothesis. This species, which is often associated with dense vegetation (Scott and Crossman 1973; Keast et al. 1978), was found resting nocturnally in greatest abundance at the inshore

site bounded by the most dense aquatic vegetation (site A), even though it did not inhabit this site during the day.

Helfman (1981) felt that the lack of intensive predation pressure was a major reason for the infrequent occurrence of well-defined diel migrations from feeding to resting areas in temperate freshwater systems. He further suggested that freshwater fishes have evolved in highly variable and short-lived ecosystems and may have evolved behavioral plasticity sufficient to alter behavioral patterns according to prevailing conditions. Stein (1979) stated that behavioral responses of prey species are dependent upon the level of predation imposed upon them. Although plasticity of movement patterns has been noted for a few species (Emery 1978; Helfman 1979), other authors have argued that activity patterns may be expressed even when fishes are not subjected to the pressures that selected for the behavior (Hobson 1972; Emery 1973). In Lake Itasca, diel nocturnal movement to sparsely vegetated inshore areas is exhibited by several prey species, the most prominent taxon involved being the mimic shiner. Our findings demonstrate that diel movements of the mimic shiner are variable among the lakes it inhabits. Furthermore, our results appear to be consistent with Helfman's (1981) assertion that modifications in prey distribution and movement patterns may result from changes in predation pressure. Further studies of diel migrations by forage fishes in lakes where predation pressures vary widely would provide a test of the general applicability of this hypothesis.

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Variation in Zinc Adsorption and Transport During Growth of *Chlamydomonas variabilis* (Chlorophyceae) in Batch Culture with Daily Addition of Zinc

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Chlamydomonas variabilis Dangeard was grown in batch culture under constant irradiance in the absence (A) or presence (B) of added zinc. Growth parameters were followed for 6 d and aliquots were removed daily from both cultures A and B for the measurement of adsorption and transport of zinc in short-term (10-min) incubations with ^{65}Zn. The concentration of EDTA-extractable zinc ($[Zn]_a$) and the flux (F) of zinc across the cell membrane both decreased with increasing culture age. Values of $[Zn]_a$ and F varied depending on when the measurements were made during the growth cycle and on the history of the inoculum. In culture B, previous growth in the presence of 7.0 μmol $Zn^{2+} \cdot L^{-1}$ resulted in larger values of $[Zn]_a$ but smaller fluxes than did growth in the absence of added zinc. Regardless of culture age, the dependence of $[Zn]_a$ on the concentration of Zn^{2+} in solution ($[Zn^{2+}]_b$) could be described by Langmuir adsorption isotherms. Conditional adsorption equilibrium constants, K_θ, were greater for cells previously grown in the presence of added zinc but showed no clear trend with culture age. Rate constants for zinc transport were smaller for cells grown with added zinc and decreased slightly with increasing culture age. The number of binding sites per unit cell surface, Q, decreased markedly with culture age, as did values obtained for $[Zn]_a$. The variation in metal adsorption and transport as a function of the physiological state of the cells should be considered when trace metal uptake is modeled and when phytoplankton are used to assess metal toxicity.

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Chlamydomonas variabilis Dangeard a été cultivé en grandes quantités dans des conditions d'irradiance uniformes et avec (A) ou sans (B) addition de zinc. Les paramètres de croissance ont été suivis durant 6 jours, et on a enlevé quotidiennement des portions aliquotes des cultures A et B afin de mesurer l'adsorption et le transport du zinc dans des incubations à court terme (10 min) avec ^{65}Zn. La concentration de zinc extractible à l'EDTA ($[Zn]_a$) et le flux (F) de zinc à travers la membrane cellulaire diminuent tous deux à mesure que la culture vieillit. Les variations observées des valeurs de $[Zn]_a$ et F dépendent du temps, dans le cycle de croissance, où les mesures ont été faites et du passé de l'inoculum. Dans la culture B, une croissance préalable en présence de 7,0 μmol $Zn^{2+} \cdot L^{-1}$ résulte en de plus grandes valeurs de $[Zn]_a$, mais en des flux moindres par rapport à une croissance sans addition de zinc. Quel que soit l'âge de la culture, la dépendence de $[Zn]_a$ sur la concentration de Zn^{2+} en solution ($[Zn^{2+}]_b$) pourrait être décrite par les isothermes d'adsorption de Langmuir. Les constantes d'équilibre d'adsorption conditionnelle, K_θ, sont plus grandes dans le cas de cellules préalablement élevées avec zinc, mais ne montrent pas de tendance nette en fonction de l'âge de la culture. Les constantes de taux de transport du zinc sont moindres pour des cellules élevées en présence de zinc et diminuent légèrement avec l'âge de la culture. Le nombre de sites de fixation par unité de surface des cellules, Q, diminue de façon marquée avec l'âge de la culture, comme c'est le cas des valeurs obtenues pour $[Zn]_a$. On devrait tenir compte de la variation de l'adsorption et du transport des métaux comme fonction de la condition physiologique des cellules dans la modélisation de l'absorption des métaux à l'état de traces, et quand on utilise le phytoplancton pour évaluer la toxicité des métaux.

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THE physiological state of phytoplankton cells grown in batch culture evolves as nutrient and light conditions change during the growth cycle. Variation in the rates of selected metabolic processes (Morris and Glover 1974; Nalewajko and Lean 1978; Bates 1981) occurring during the lag, exponential, and stationary phases of growth results in different chemical compositions of phytoplankton (Sakshaug and Holm-Hansen 1977) and possibly in different sensitivities to chemical stresses during these phases. This has profound implications for studies that draw conclusions from measurements taken only once during the growth cycle.

The batch culture system is used in the majority of toxicity studies employing algae, and measurements are often made within the period of exponential growth, although it is known that metal toxicity can vary depending on the age and therefore on the physiological state of the culture (Gibson 1972; Hutchinson and Stokes 1975; De Filippis and Pallaghy 1976). Metal toxicity may also depend on the stage in the cell division cycle; this will be important if cells in the batch culture are dividing synchronously (Kanazawa and Kanazawa 1969; Steemann Nielsen and Kamp-Nielsen 1970; Hornung et al. 1981). Less frequently, problems of varying physiological state are minimized by using continuous or semicontinuous culture systems (Kayser 1976; Conway 1978; Li 1979; Cloutier-Mantha and Harrison 1980; Bates et al. 1982). Few studies have followed the accumulation of a trace metal throughout the growth cycle in batch culture (Davies 1973, 1974; Cossa 1976; Jennings and Rainbow 1979; Butler et al. 1980; Cain et al. 1980). No studies were found that measured the ability of cells to accumulate metals during short-term incubations at different stages in the growth cycle. It is clear that variations in the cells' capacity to accumulate trace metals must be understood before standard tests can be used to assess metal toxicity.

It is useful to be able to distinguish the quantity of trace metal adsorbed onto the cell surface from that actually transported across the membrane to enable an evaluation of mechanisms of toxicity and of accumulation. The quantity of adsorbed versus transported metal can be determined in a desorption step by washing the cells in a solution containing a strong chelator (Davies 1973; Cossa 1976; Kremling et al. 1978; Hawkins and Griffiths 1982). Using an EDTA-extraction procedure, Bates et al. (1982) obtained values for an equilibrium constant (K_a) for the adsorption of zinc onto the cell surface, the maximum concentration (Q) of adsorbed zinc, and a rate constant (k_c) for the transport of zinc by *Chlamydomonas variabilis* and *Scenedesmus subspicatus* preconditioned in a semicontinuous culture. The magnitude and degree of variation of K_a and k_c are important for modeling trace metal uptake by phytoplankton cells. The present work documents the variation in zinc adsorption and transport parameters (K_a, Q, k_c) measured daily in batch culture throughout the growth cycle of *C. variabilis* grown in either the presence or absence of added zinc. As a micronutrient essential to life, zinc is most commonly associated with the function of certain enzymes (Vallée 1977). It is also a pollutant in some aquatic ecosystems (Förstner and Wittmann 1981), particularly in certain freshwater lakes and streams of Canada, the world's largest zinc producer and ranked third in zinc refining capacity (Spear 1981).

Materials and Methods

Chlamydomonas variabilis Dangeard (Chlorophyceae) strain 511/5 (ex-Centre de Recherche Hydrobiologique de Gif-sur-Yvette, France) was maintained axenically for 19 mo in AAP medium (Payne 1975) in the absence of added zinc. Observations indicated that cell morphology and division rates were not adversely affected by the absence of added zinc. The zinc required for growth probably originated from general contamination, although no zinc could be detected by graphite furnace atomic absorption spectrophotometry ($<8 \times 10^{-9}$ mol $Zn \cdot L^{-1}$) in the culture medium prior to growth of the algae (Bates et al. 1982). Two experimental 5-L batch cultures ("A" and "B") were grown at 20°C under a constant irradiance of approximately 120 $\mu E \cdot m^{-2} \cdot s^{-1}$ provided by two banks of cool white fluorescent bulbs; the pH was maintained at 7.0 ± 0.2 with a pH control system using automatic additions of carbon dioxide (Bates et al. 1982). Batch culture A contained no added zinc; culture B contained stable zinc at 7.7 $\mu mol \cdot L^{-1}$ (~7.0 $\mu mol\ Zn^{2+} \cdot L^{-1}$), added on day 0 when the system was inoculated with *C. variabilis* obtained from a stock culture in the early stationary phase. To minimize iron oxide precipitation in the culture medium, the acid trace metal mix and macronutrients were autoclaved separately and were aseptically combined after cooling. Growth parameters were followed daily for 6 d in both cultures; zinc uptake by phytoplankton cells was measured continuously (daily) in culture B throughout the entire growth cycle. In addition, aliquots were removed daily from both cultures to measure the adsorption and transport of zinc in short-term (10-min) experiments.

In the short-term incubation experiments, 40-mL aliquots, taken daily in duplicate from cultures A and B, were centrifuged for 10 min at approximately 500 × g in polycarbonate centrifuge tubes. The supernatant solution was removed by suction using a Pasteur pipet, and the pellet was resuspended in an equivalent volume of unautoclaved AAP medium (pH 7.0) containing total zinc at 18.5 $\mu mol \cdot L^{-1}$, 3.7 MBq $^{65}Zn \cdot L^{-1}$ (New England Nuclear Corp.), and varying concentrations of EDTA to give the desired initial concentrations of free ionic zinc (Table 1). The incubation solutions had been equilibrated for approximately 20 h before use. After a 10-min incubation in darkness at 20°C, the sample was centrifuged for 10 min at approximately 500 × g, and the supernatant was removed for determination of ^{65}Zn radioactivity; this gave $[Zn]_b$, the total concentration of zinc remaining in the bulk solution after the 10-min incubation period. The additional incubation time with zinc during the 10-min centrifugation period was not taken into account in the calculations. The unwashed pellet was then resuspended in 10.0 mL of a solution (pH 7.0) containing 10^{-4} mol $EDTA \cdot L^{-1}$ plus 0.6 mmol $CaCl_2 \cdot L^{-1}$ (added to adjust the ionic strength) for 10 min in darkness. After centrifuging for 10 min, the supernatant was removed for determination of ^{65}Zn radioactivity; this gave $[Zn]_a$, the concentration of zinc previously adsorbed onto the cell surface, which is operationally defined as the concentration of zinc extracted by the EDTA (Bates et al. 1982). The unwashed pellet was then transferred to a test tube with 5.0 mL of deionized water for determination of ^{65}Zn radioactivity; this gave $[Zn]_i$, the con-

TABLE 1. Concentrations of EDTA added to the AAP medium and the corresponding concentrations of initial computed free ionic zinc ($[Zn^{2+}]$) in the solutions used in the short-term experiments. Concentration of total zinc was 18.5 $\mu mol \cdot L^{-1}$.

Solution No.	[EDTA] ($\mu mol \cdot L^{-1}$)	$[Zn^{2+}]$ ($\mu mol \cdot L^{-1}$)
1	14.9	3.6
2	14.1	4.4
3	12.4	6.1
4	9.8	8.6
5	7.7	10.7
6	6.6	11.8

centration of zinc transported across the cell membrane, which is operationally defined as the concentration of zinc remaining within the cells after extraction with EDTA (Bates et al. 1982). The flux, F (moles per square centimetre per second), of zinc across the cell membrane can be expressed as

$$(1)\ F = \frac{d[Zn]_c}{dt} \cdot \frac{W}{S}$$

where $[Zn]_c$ has the units of moles per gram dry weight, W is the cellular dry weight (grams per cell), S is the cellular surface area, and dt (= 600 s) is the incubation time. Assuming a sphere of radius r and of density ρ (equal to 1) and substituting $S = 4\pi r^2$, $V = \frac{4}{3}\pi r^3$, and $W = \rho V$ into equation (1) leads to

$$(2)\ F = \frac{d[Zn]_c}{dt} \cdot \frac{W^{1/3}}{4.84}.$$

The value of $[Zn^{2+}]_b$ (the concentration of free ionic zinc remaining after a 10-min incubation period) was computed with a chemical equilibrium model that took into account $[Zn]_b$ and the chemical composition of the AAP medium (Bates et al. 1982). The minimal effects of centrifugation and of EDTA extraction on zinc accumulation by *C. variabilis* have been discussed previously (Bates et al. 1982).

As mentioned above, zinc uptake by the cells was measured continuously over the growth cycle in batch culture B itself. Duplicate daily aliquots were removed from culture B and $[Zn]_a^*$, $[Zn]_c^*$, and $[Zn^{2+}]_b^*$ were measured as described above. An asterisk is used to distinguish the concentrations observed in culture B where stable zinc was used from those observed after the short-term incubations using aliquots withdrawn from cultures A and B where radioactive zinc was used.

Radioactivity of ^{65}Zn was determined with a gamma spectrophotometer (LKB Wallac model SC-26, PP-67). Zinc in culture B was analyzed using a flame atomic absorption spectrophotometer (Varian Techtron model AA-575 ABQ). Cell numbers were determined with a model T_A Coulter counter. Cell dry weights were determined twice daily with an electrobalance (Mettler model ME30) after filtration of culture aliquots onto preweighed Nuclepore filters (1.0 μm, 25-mm diameter) and drying at 75°C to a constant weight.

Results

The presence of free ionic zinc at an initial concentration of 7.0 $\mu mol \cdot L^{-1}$ depressed the division rate of *C. variabilis* in culture B by approximately 30% relative to culture A and reduced the cell yield obtained during the stationary phase by approximately 40% when calculated from cell concentration (Fig. 1a) and by approximately 70% when calculated from cellular dry weight (Fig. 1b). The dry weight per cell decreased at about the same rate during the early exponential phase whether the cells were grown in the presence or absence of added zinc (Fig. 1c). However, during the stationary phase the increase in dry weight per cell was greater in the culture grown in the absence of added zinc. In culture B, $[Zn]_a^*$ decreased rapidly during exponential growth and remained stable during the stationary phase, $[Zn]_c^*$ increased steadily but at a decreasing rate as the culture aged, and $[Zn^{2+}]_b^*$ decreased steadily throughout the growth cycle (Fig. 2). A budget of total zinc (the sum of $[Zn]_b^*$, $[Zn]_a^*$, and $[Zn]_c^*$) remained constant to within 2%, indicating that no significant amount of metal was adsorbed onto or desorbed from the glassware.

For the short-term incubation periods with aliquots withdrawn from cultures A and B, $[Zn]_a$ decreased greatly with increasing culture age during the exponential growth phase for all of the zinc concentrations studied and attained a plateau of low $[Zn]_a$ during the stationary phase (Fig. 3a, 4a). This pattern parallels that found for the change in $[Zn]_a^*$ during the growth cycle in culture B (Fig. 2). For 10-min incubation periods, F (or $[Zn]_c$) consistently decreased during the period extending from the exponential to the stationary phase for algae from cultures A (Fig. 3b) and B (Fig. 4b) in conformity with the decreasing rate of zinc transport with culture age (Fig. 2); the decrease was most evident for the higher zinc concentrations studied.

Although the patterns described above for the change in $[Zn]_a$ and F measured during short-term incubations over the growth cycle were similar in cultures A and B, the magnitudes of $[Zn]_a$ and F differed depending on whether the cells were conditioned with or without added zinc: previous growth in the presence of 7.0 $\mu mol\ Zn^{2+} \cdot L^{-1}$ resulted in a larger $[Zn]_a$ (Fig. 4a) but a smaller F (Fig. 4b) than did growth in the absence of added zinc (Fig. 3).

Whether the cells were grown initially in the absence (Fig. 5a) or the presence (Fig. 6a) of added zinc, $[Zn]_a$, determined after a 10-min incubation period, was a function of $[Zn^{2+}]_b$ (and not of $[Zn]_b$) and could generally be described by a Langmuir adsorption isotherm:

$$(3)\quad [Zn]_a = \frac{Q[Zn^{2+}]_b}{K_\theta^{-1} + [Zn^{2+}]_b}$$

where K_θ is an adsorption equilibrium constant (litres per mole) for the adsorption of zinc onto the cell surface and Q is the maximum concentration (moles per square centimetre) of EDTA-extractable zinc. Values of Q (Table 2) decreased during the period extending from the exponential to the stationary growth phase. Values of K_θ (Table 2) were slightly lower in the cells grown in the absence than in the presence of added zinc, but showed no clear trend in variation with

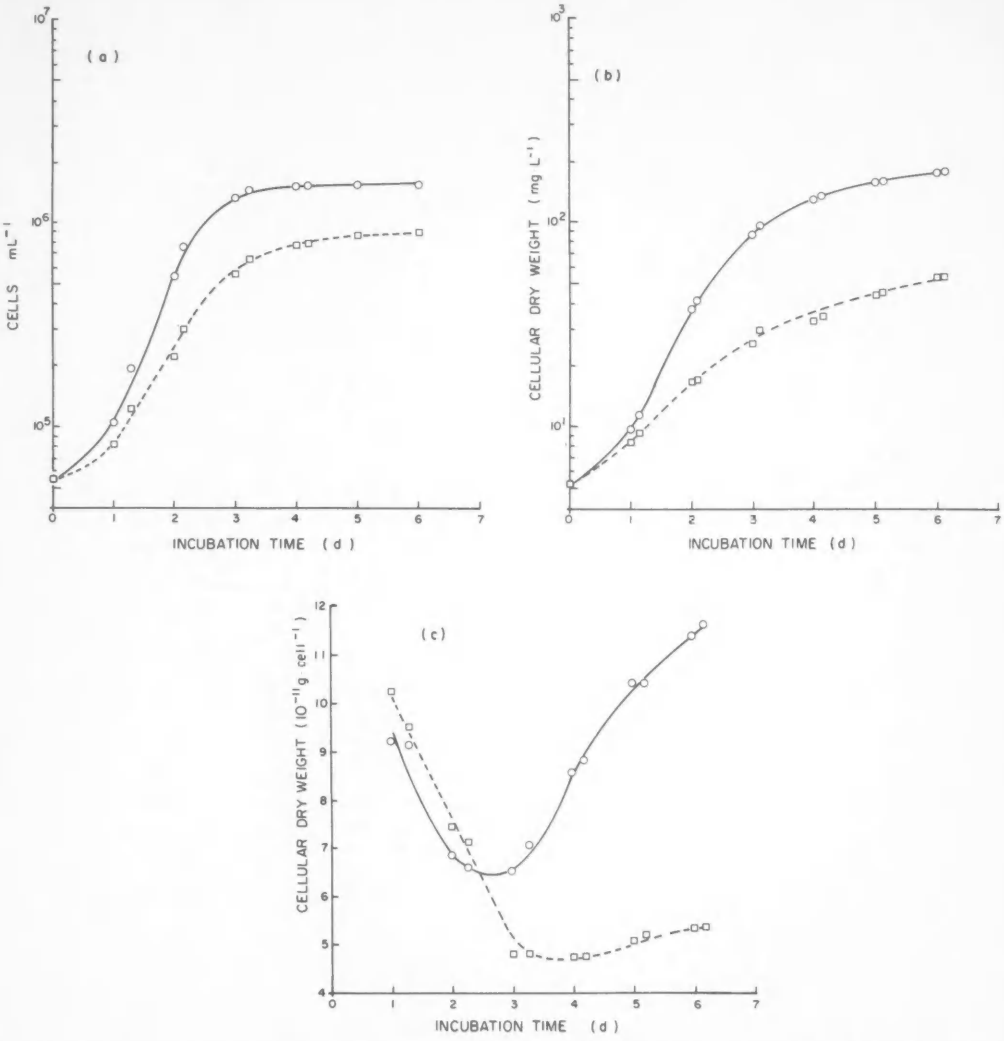

FIG. 1. Growth curves of *Chlamydomonas variabilis* in the absence of added zinc (○, culture A) and in the presence of an initial free ionic zinc concentration of approximately 7.0 μmol·L^{-1} (□, culture B). (a) Cell concentration; (b) cellular dry weight; (c) dry weight per cell.

culture age.

The flux of zinc across the cell membrane for short-term incubations was also a function of $[Zn^{2+}]_b$ (Fig. 5b, 6b) and could be described by

$$(4) \quad F = k_c[Zn^{2+}]_b$$

where k_c is a rate constant (centimetres per second) for the transport of zinc across the cell membrane. Values of k_c (Table 2) generally decreased with increasing culture age and were smaller for cells conditioned in the presence of added zinc, except at day 1.

Discussion

A reduction in cell yield of *C. variabilis* in the presence of an elevated concentration of zinc (Fig. 1a, 1b) has been observed previously (Bates et al. 1982); this is believed to

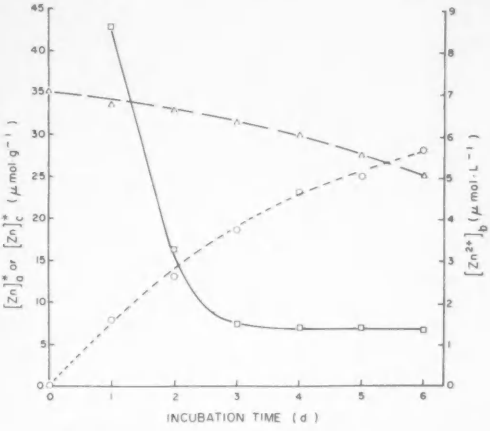

FIG. 2. Changes with incubation time in the concentration of free zinc remaining in solution (△), EDTA-extractable zinc (□), and transported zinc (○) for *Chlamydomonas variabilis* growing in batch culture B.

be due to incomplete use of phosphorus both in the incubation medium and within the cell (Bates et al., unpublished). The present decrease in the division rate of *C. variabilis* by approximately 30% in the presence of approximately 7.0 μmol $Zn^{2+} \cdot L^{-1}$ (Fig. 1a, 1b) differs from the findings of our previous study (Bates et al. 1982) in which division rates were not influenced by up to approximately 12.3 μmol $Zn^{2+} \cdot L^{-1}$. This difference could be due to a possible sensitivity to zinc acquired by the stock culture of algae that was grown in the absence of added zinc for a longer period (19 mo as opposed to 2 mo). Such a loss in metal tolerance was reported for the chlorophyte *Scenedesmus* grown in the absence of copper (Stokes and Dreier 1981). Furthermore, algae in the present study were grown in continuous light as opposed to a light–dark cycle as in the previous work (Bates et al. 1982); cadmium is more toxic to the chlorophyte *Coelastrum proboscideum* grown in continuous light than when a photoperiod is used (Hornung et al. 1981). Continuous irradiance was used in the present study to avoid obtaining a synchronous culture and the associated problem of different sensitivities to trace metals depending on the stage in the cell division cycle (Kanazawa and Kanazawa 1969; Steemann Nielsen and Kamp-Nielsen 1970). By comparison, the division rate of the freshwater chlorophyte *Scenedesmus quadricauda* was reduced by 50% in the presence of 7.4 μmol $Zn^{2+} \cdot L^{-1}$ in continuous light (Petersen 1982).

During the stationary phase the dry weight per cell is lower in the presence of added zinc than in the control culture (Fig. 1c); this result suggests that in the presence of added zinc less organic matter was synthesized, respiration rates were greater, or excretion of organic matter increased (cf. Butler et al. 1980). The dry weight per cell was more closely related to transported zinc than to EDTA-extractable zinc; values of $[Zn]_a^*$ (Fig. 2) and the difference in cellular dry weights between cultures A and B (Fig. 1b) both increased with incubation time whereas values of $[Zn]_a^*$ decreased (Fig. 2).

The finding that values of $[Zn]_a$ as a function of $[Zn^{2+}]_b$ for *C. variabilis* could be described by Langmuir adsorption isotherms (Fig. 5a, 6a) is in accordance with Davies (1973) and Bates et al. (1982). Nevertheless, *C. variabilis* exhibits wide variations in the ability to adsorb zinc depending on when the measurements are made during the growth cycle. Most striking is the decrease in the values of $[Zn]_a$ as the culture progresses from the exponential to the stationary phase (Fig. 3a, 4a). This decrease in the cells' ability to adsorb zinc as the culture ages may be caused by physicochemical changes in the growth medium or by changes in the physiology of the algae. A possible chemical alteration of the medium could be caused by the excretion of organic matter, which could complex with the zinc, thereby favoring a desorption of the metal (cf. Butler et al. 1980). However, in the present study the old growth medium was removed by centrifugation prior to measuring $[Zn]_a$ for both cultures A and B, and unless the cells were able to excrete material rapidly during the 10-min incubation period, then the concentration of extracellular matter should be low in the incubation solution. This may not be the case for the cells grown in the continual presence of zinc (culture B, $[Zn]_a^*$).

A second possible alteration of the medium could be caused by the precipitation of iron hydroxide, as the AAP medium is supersaturated by a factor of about two with respect to iron hydroxide ($K_{sp} = 10^{-37.1}$ for freshly precipitated amorphorus hydroxide; Whittemore and Langmuir 1975). Care was taken to minimize the formation of precipitates by autoclaving separately the iron-containing trace metal mix and the remainder of the growth medium. Nevertheless, if such precipitates did form during the growth period of the algae, they may be expected to adsorb onto the surface of the algae (Anderson and Morel 1982). It may, in fact, be argued that the majority of the measured EDTA-extractable zinc is actually adsorbed onto iron hydroxide adhering to the cells (F. M. M. Morel, Massachusetts Institute of Technology, personal communication), rather than onto sites that form an integral part of the cell wall and/or membrane. The cell quota for iron was calculated by dividing the concentration of dissolved iron (determined by flame atomic absorption spectrophotometry) that disappeared from the growth medium (from day 0 to the stationary phase) by the increase in cell number over the same period; typically, this value was 1.5×10^{-16} mol Fe·cell^{-1}, which closely corresponds to the minimum cell quota for growth (1.3×10^{-16} mol Fe·cell^{-1}) of *Thalassiosira weissflogii* (Anderson and Morel 1982), suggesting that the iron was taken up and not coagulated onto the surface of the cells. If, in the worst case, the dissolved iron that disappeared from the growth medium is assumed to be coagulated onto the cells' surface, a hypothetical concentration of iron coagulated onto the cells' surface ($[Fe]_s$) can be estimated; the ratio $[Zn]_a/[Fe]_s$ then varies from 0.26 to 2.28. These values are clearly too high to suggest that zinc is adsorbed onto iron hydroxide. It seems, therefore, that under the present conditions the observed EDTA-extractable zinc originates from adsorption sites that form an integral part of the cell wall and/or membrane, rather than from sites provided by precipitated iron hydroxides.

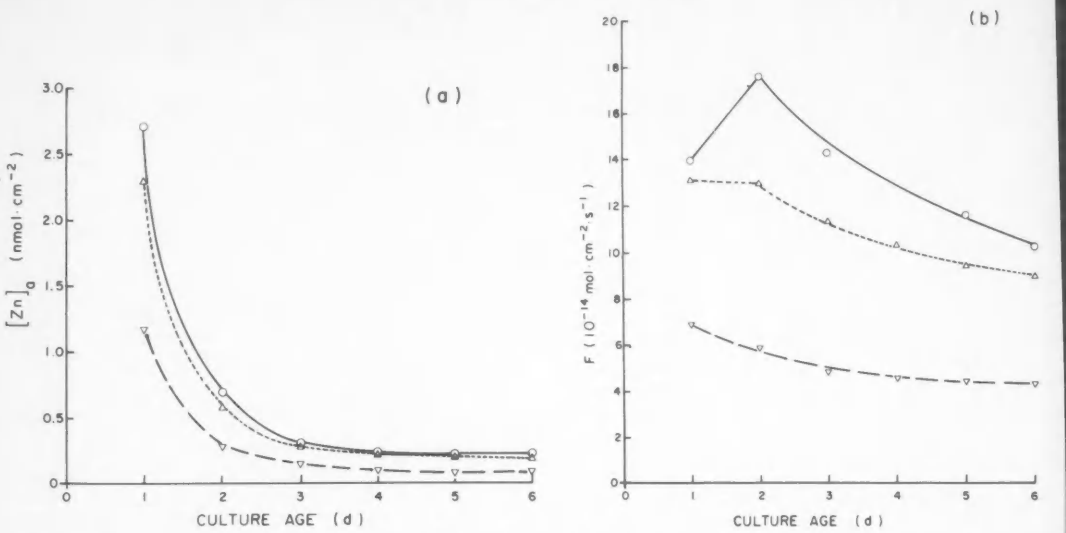

FIG. 3. Changes with culture age in the concentration of (a) EDTA-extractable and (b) transported zinc for *Chlamydomonas variabilis* during a 10-min incubation period in the presence of 3.7 (▽), 8.6 (△), and 10.7 (○) μmol $Zn^{2+}\cdot L^{-1}$. Measurements made in the presence of 4.4, 6.1, and 11.8 μmol $Zn^{2+}\cdot L^{-1}$ showed the same trend but are excluded for clarity. Cells were obtained from culture A, grown in the absence of added zinc.

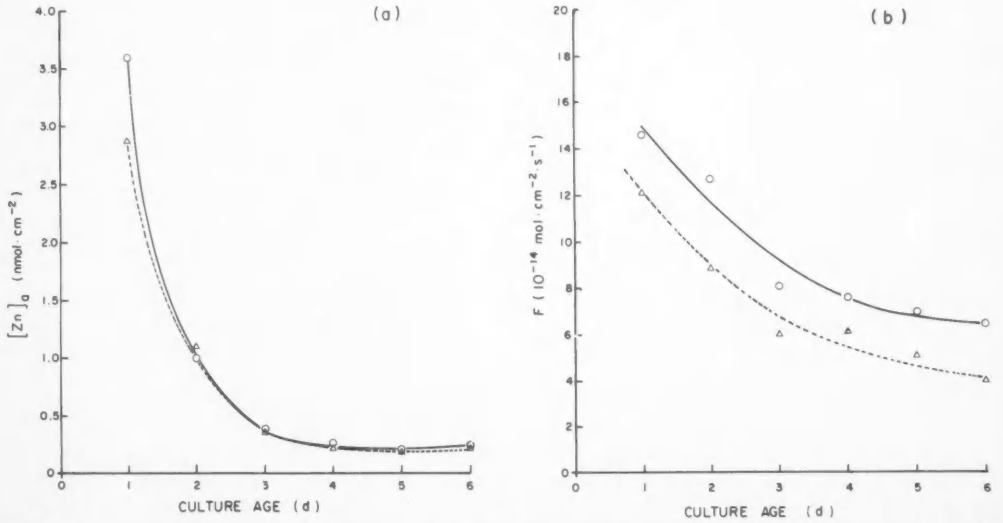

FIG. 4. Changes with culture age in the concentration of (a) EDTA-extractable and (b) transported zinc for *Chlamydomonas variabilis* during a 10-min incubation period in the presence of 8.6 (△) and 10.7 (○) μmol $Zn^{2+}\cdot L^{-1}$. Cells were obtained from culture B, grown in the presence of approximately 7.0 μmol $Zn^{2+}\cdot L^{-1}$.

As there is thus little evidence to suggest that physico-chemical changes in the growth medium are responsible for the observed change in $[Zn]_a$ with culture age, possible physiological explanations must be examined. The decrease in the cells' ability to adsorb zinc may be related to structural changes occurring on the cell surface as the culture ages. These changes may arise by a sloughing off of portions of the outer cell surface as the cells divide (Roberts et al. 1972).

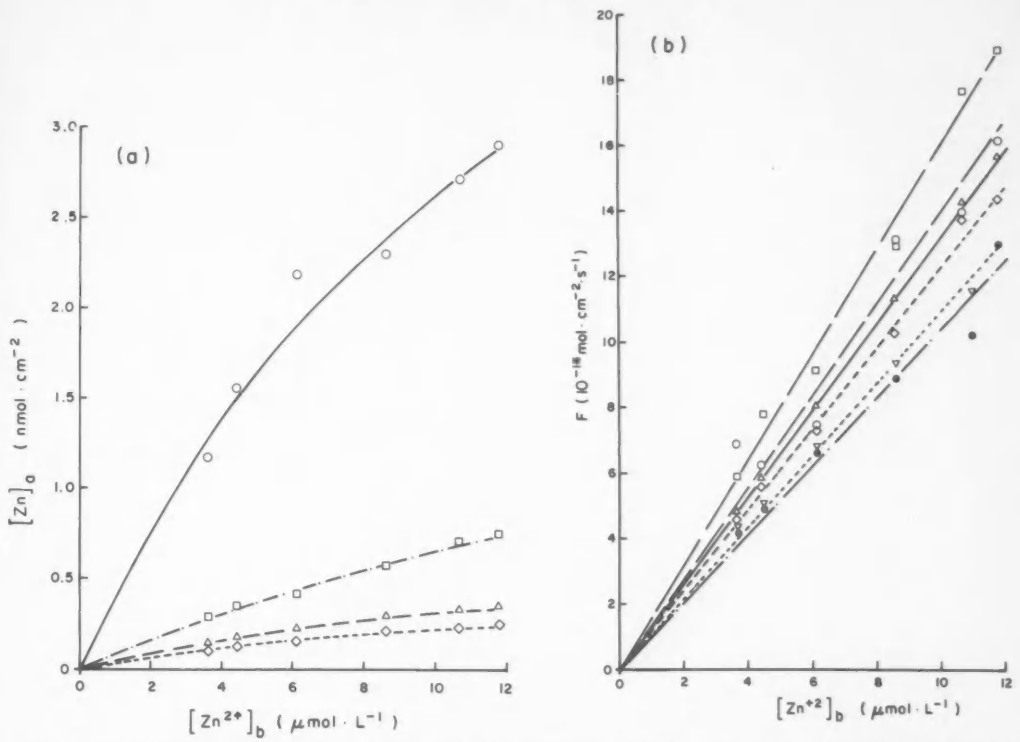

FIG. 5. Relationships for *Chlamydomonas variabilis* between the concentration of (a) EDTA-extractable and (b) transported zinc and the concentration of computed free ionic zinc remaining in solution after a 10-min incubation period. Measurements were made on day 1 (○), 2 (□), 3 (△), 4 (◇), 5 (▽), and 6 (●) for cells obtained from culture A, grown in the absence of added zinc. Curves for $[Zn]_a$ were constructed with equation (3) and the constants given in Table 2.

Different functional groups representing different bonding characteristics (Crist et al. 1981) may also be found on the cell surface depending on the phase of the growth cycle. The functional groups may change as a consequence of the varying cellular chemical composition found at different stages in the growth cycle (Sakshaug and Holm-Hansen 1977). Davies (1974) suggested that the changes in Freundlich isotherm constants for mercury adsorption by *Isochrysis galbana* reflected changes in adsorption sites on the cell surface due to alterations in cell metabolism as the culture progressed through its growth cycle. Indeed, Lukiewicz and Korohoda (1965) found that the electrophoretic mobility of *Chlorella* changes during its growth; actively growing cells exhibited a high negative charge density on the cell surface, whereas the density of negative charges dropped with a decrease in growth rate. This change in charge density was attributed to alterations in the protein and polysaccharide components of the cell wall during the life cycle of *Chlorella*. Such a decrease in the negative charge density as the culture ages indicates that the surface of the membrane is modified during growth; the change in the capacity of the cell surface to adsorb zinc (Fig. 3a, 4a) might be related to this change in structure. That the change in electrophoretic mobility with growth rate is a feature common to both plant and animal cells (Lukiewicz and Korohoda 1965) suggests that the changing ability of the cell surface to adsorb zinc, found for *C. variabilis*, may also be common to other organisms.

A change in the nature of binding sites should be reflected in the affinity (K_a) values, whereas a change in the number of sites should be reflected in the Q values. The slight difference in K_a values between cultures A and B (Table 2) suggests that conditions on the surface of the algae (electrical fields, relative number of functional groups, steric hindrance) are slightly different for cells grown in the two cultures. On the other hand, the relatively constant K_a values for each culture indicate that the nature of the functional groups does not change during the growth cycle. In contrast, the decrease in Q values with the age of both cultures (Table 2) strongly suggests that the quantity of binding sites decreases with increasing culture age.

Values for zinc transport, F, were also influenced by the culture age and previous growth in the presence or absence of added zinc, although less so than values for EDTA-extractable zinc. The slight decrease with culture age in the

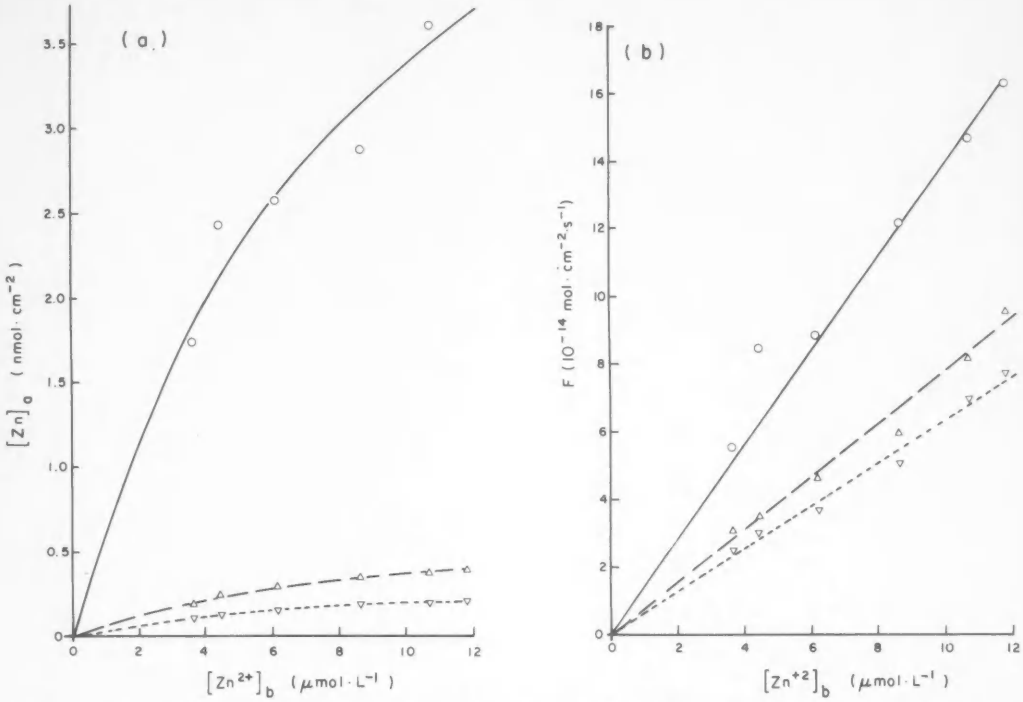

FIG. 6. Relationships for *Chlamydomonas variabilis* between the concentration of (a) EDTA-extractable and (b) transported zinc and the concentration of computed free ionic zinc remaining in solution after a 10-min incubation period. Measurements were made on day 1 (○), 3 (△), and 5 (▽) for cells obtained from culture B, grown in the presence of approximately 7.0 μmol $Zn^{2+} \cdot L^{-1}$. Curves for $[Zn]_a$ were constructed with equation (3) and the constants given in Table 2.

TABLE 2. Equilibrium constants for EDTA-extractable zinc and rate constants for zinc transport by *Chlamydomonas variabilis* obtained after a 10-min incubation period (data from Fig. 5 and 6).

Parameter	Culture[a]	Culture age (d)					
		1	2	3	4	5	6
Q^b (10^{-10} mol · cm^{-2})	A	64.5	26.9	8.3	4.9	—[c]	—[c]
	B	64.7	—[d]	6.7	—[d]	3.4	—[d]
$K_a{}^b$ (10^4 L · mol^{-1})	A	6.8	3.22	6.0	8.2	—[c]	—[c]
	B	10.9	—[d]	11.9	—[d]	13.6	—[d]
$k_t{}^e$ (10^{-5} cm · s^{-1})	A	1.4	1.6	1.3	1.2	1.1	1.1
	B	1.4	1.1	0.8	0.7	0.7	0.6

[a]Culture A grown in the absence of added zinc; culture B grown with 7.0 μmol $Zn^{2+} \cdot L^{-1}$.
[b]Calculated from linear transformation of equation (3).
[c]Calculations not possible.
[d]Measurements not made.
[e]Calculated from equation (4).

ability to transport zinc (Fig. 3b, 4b) may be due to an accompanying decrease in intracellular protein, an efficient ligand (Davies 1973; 1974; Cossa 1976). During the short-term incubations, more zinc was transported into cells grown in the absence of added zinc (Fig. 3b) than into cells previously conditioned in the presence of zinc (Fig. 4b). This suggests

that previously transported zinc may occupy intracellular binding sites, thus slowing further zinc transport.

At the relatively high ionic zinc concentrations used in the present study, zinc adsorption and transport appear to be two independent processes. Indeed, the relationship between F and $[Zn^{2+}]_b$ is linear, regardless of culture age (Fig. 5b, 6b); if F were a function of $[Zn]_a$, then the relationship between F and $[Zn^{2+}]_b$ would show a curvature at the higher ionic zinc concentrations, according to the measured value of K_a. In addition, at a given $[Zn^{2+}]_b$ the slight decrease in F with culture age (Fig. 3b, 4b) does not appear to follow the sharp decrease in $[Zn]_a$ (Fig. 3a, 4a). Under the present conditions, therefore, it appears that zinc transported into the cell is not primarily a function of the total "adsorbed" zinc fraction. This result, which is in accordance with that of our previous study (Bates et al. 1982), should not be construed as an indication that carrier-mediated transport of zinc is not occurring. We suspect that such transport may indeed be important at very low concentrations of free ionic zinc but that it is swamped by the passive diffusion of zinc at the concentrations studied in the present investigation. EDTA-extractable zinc presumably includes not only zinc bound to those specific high-affinity sites responsible for zinc transport at low ambient free zinc concentrations, but also zinc held at nonspecific sites on the cells' surface. If this were the case, then the absence of a relationship between F and $[Zn]_a$ would not be surprising.

The total zinc concentrations used in this study are relatively high compared with those found in natural waters. However, in natural waters at pH 7.0, total zinc concentration is approximately equal to free zinc concentration, as the natural inorganic and organic ligands do not complex zinc appreciably at that pH (Spear 1981). In contrast, there were larger differences between total and free zinc concentrations in our study due to the use of a strong ligand, EDTA. A comparison between $[Zn^{2+}]$ used in this study and total dissolved zinc concentration found in natural waters (Förstner and Wittmann 1981) indicates that they overlap in the lower range. If our physiological interpretation for the changes in the ability for phytoplankton cells to adsorb zinc is correct, then one may expect to see similar responses to other metals, in addition to zinc, in natural populations of phytoplankton.

Many factors influence trace metal availability to phytoplankton: e.g. metal speciation, pH, water hardness, major nutrients, and synergism–antagonism among metals (Huntsman and Sunda 1980; Rai et al. 1981). The physiological condition of the algae is an additional factor that should be considered when carrying out algal bioassays of trace metals using laboratory or natural populations of phytoplankton. The physiology of laboratory cultures of algae may be controlled for the purpose of studying trace metals by using continuous culture techniques (Li 1979; Cloutier-Mantha and Harrison 1980) or by insuring that measurements are consistently made during the same phase of the growth cycle in an asynchronous batch culture. It is more difficult to assess the physiological state of natural populations of algae (Sakshaug and Holm-Hansen 1977; Bates 1981). Nevertheless, if it is assumed that a spectrum of algal physiological states is found in nature, then one may suppose that an algal population, regardless of the other factors that influence metal bioavailability, would exhibit a spectrum of responses to trace metals as a function of physiological state.

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Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles-de-la-Madeleine

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La population de homards des lagunes des Îles-de-la-Madeleine a été étudiée au cours des deux saisons estivales 1978 et 1979, en utilisant la technique de marquage/recapture par casier conventionnel et par observation en plongée. Les résultats obtenus montrent l'existence de migrations actives du homard entre la côte et les lagunes au printemps (entre la mi-mai et la fin juin) et à l'automne (entre le début et la fin d'octobre). Ces migrations saisonnières sont liées au réchauffement et au refroidissement des masses d'eau. Suite à sa sortie des lagunes, nous avons pu montrer qu'une grande partie du homard lagunaire demeurait à proximité des embouchures, ce qui expliquerait les retours élevés à la lagune le printemps suivant. Pour expliquer les pourcentages de mâles beaucoup plus élevés dans les lagunes que sur la côte, nous suggérons l'existence d'une sélectivité positive en ce qui concerne la mobilité des mâles lors de la période de migration du printemps. Par contre, les différences dans les structures de taille notées entre les lagunes et la côte sont vraisemblablement causées par des variations dans la pression de pêche commerciale.

MUNRO, J., ET J.-C. THERRIAULT. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles-de-la-Madeleine. Can. J. Fish. Aquat. Sci. 40: 905 – 918.

During the summers of 1978 and 1979, the lobster population of the lagoons of the Magdalen Islands was investigated using tag/recapture techniques and direct observations by divers. The results show an active migration pattern of lobsters into (from mid-May to the end of June) and out of (from the beginning to the end of October) the lagoons, linked to seasonal water temperature variations. Following migration out of the lagoons the lobster stay mainly close to the entrance of the lagoons; this principally explains the high percentage of returns to the lagoon the following spring. To explain the much higher percentage of males in the lagoons than in the coastal area, we suggest the existence of a positive selection for mobility of the males during the spring migration. However, the differences in size structure distribution between the coast and the lagoons are mostly due to variations in commercial fishing pressure.

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L'EXISTENCE de migrations effectuées par le homard (*Homarus americanus*) vers la côte au printemps et vers le large à l'automne a été documentée pour les côtes des Iles-de-la-Madeleine (Templeman 1936; Montreuil 1960; Bergeron 1967; Anonyme 1978), de la Baie des Chaleurs (Corrivault 1948) et de la Baie de Narragansett (Jeffries et Johnson 1974). De même a-t-on rapporté qu'une proportion importante de la population de homards localisée à la limite du plateau continental montrait un mouvement migratoire de grande amplitude associé aux variations saisonnières de la température (Uzmann et al. 1977).

De telles migrations entre la côte et les lagunes des Îles-de-la-Madeleine ont également été rapportées par Templeman (1936) qui en plus a révélé l'existence de deux périodes de mues dans les lagunes. Montreuil (1960) et Bergeron (1967) ont fourni des informations sur la dispersion côtière du homard après sa sortie des lagunes à l'automne et ils ont également indiqué que comparé à la côte, le pourcentage de mâles était toujours plus élevé dans les lagunes.

Les lagunes, étant séparées de l'ensemble du littoral des

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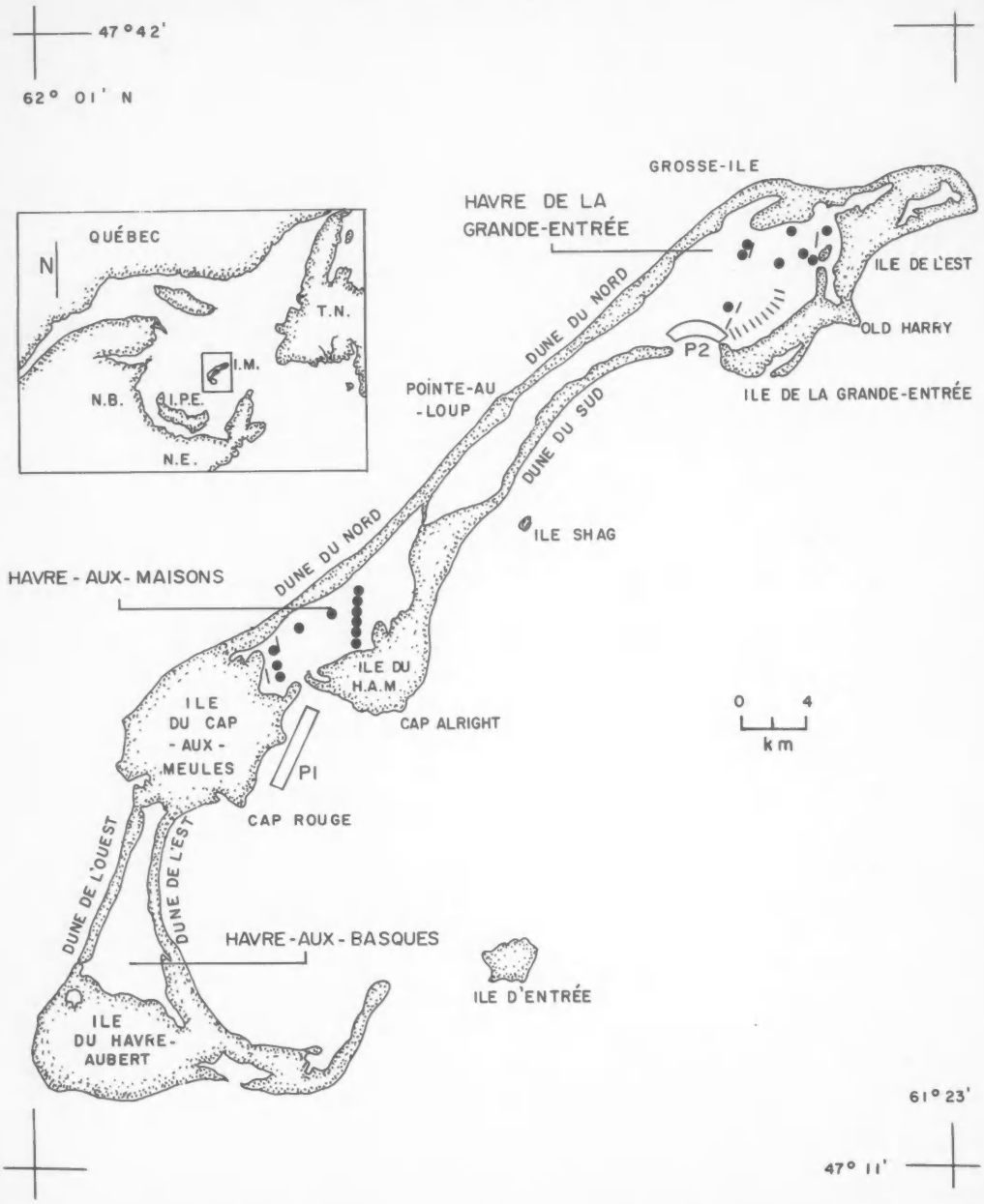

FIG. 1. Carte des Îles-de-la-Madeleine localisant les stations d'échantillonnage par casier (●) et les transects de plongée (/). Les pêches aux embouchures du Havre-aux-Maisons (P1) et du havre de la Grande-Entrée (P2) (Burton et al. 1980) sont également localisées.

Îles-de-la-Madeleine par des passages étroits, constituent certainement une situation expérimentale idéale pour étudier le phénomène de la migration du homard. Nous avons donc voulu profiter de ce laboratoire naturel pour examiner les relations qui existent entre ces migrations et la température des masses d'eau, ainsi que pour essayer d'expliquer pourquoi les caractéristiques de la population lagunaire sont différentes de celles de la côte.

Matériel et méthodes

Aire d'Étude

Le milieu lagunaire des Îles-de-la-Madeleine (fig. 1) couvre près de 100 km carrés de zone intertidale et infralittorale ayant une profondeur maximale de 11 m. Cet habitat marin caractérisé par des fonds vaseux et sablonneux, équivaut en surface au huitième du littoral côtier des Iles limité par l'isobathe de 20 m. La superficie de la lagune du havre de la Grande-Entrée est d'environ le double (50 km^2) de celle du Havre-aux-Maisons (25 km^2), tandis que les rapports de volumes sont de plus de 3 pour 1. Les amplitudes moyennes de marée de 0,58 et 0,67 m caractérisent le havre de la Grande-Entrée (Bourget 1976) et le Havre-aux-Maisons (Munro et Therriault 1981), et permettent des échanges respectifs de l'ordre de 16 et 22 % du volume total par cycle de marée.

La caractéristique océanographique principale des lagunes est une grande homogénéité verticale observée dans tous les facteurs étudiés (température, salinité, chlorophylle et sels nutritifs), du moins pour la période estivale (Auclair 1977; Ministère des Pêches et des Océans, données non publiées). Entre mai et novembre, la température de l'eau varie entre 2 et 23°C et la salinité entre 22 et 31 ‰ (Munro et Therriault 1981).

Munro et Therriault (1981) ont estimé que la population de homards en période estivale (pour les longueurs de céphalothorax $\geq$ 70 mm) se chiffre autour de 90 000 individus pour le havre de la Grande-Entrée et de 37 000 individus pour le Havre-aux-Maisons: les coefficients de variation sur ces estimations étant de moins de 18 %.

Échantillonnage par Plongée

Les plongées étaient effectuées par deux plongeurs qui parcouraient ensemble des transects balisés d'une longueur variant entre 200 et 1 000 m (fig. 1). La visibilité locale déterminait la largeur effective de chaque transect (3 à 6 m) et des corrections à cet effet ont été apportées lors du calcul des densités (nombre de homards par kilomètre au carré). Dans le havre de la Grande-Entrée, en 1978, 86 homards (mâles et/ou femelles) furent observés sur une surface totale de 50 km^2. Dans le Havre-aux-Maisons, en 1979, on en a compté 185 sur 23 km^2.

Échantillonnage par Casiers

La pêche était effectuée à l'aide de lignes de 5 ou 10 casiers conventionnels boettés avec un hareng ou un maquereau et mouillés pour une période d'au moins 24 h. Les captures provenant de pêches de plus de 24 h ont été standardisées à une journée de pêche (voir Munro et Therriault 1981). Diverses mesures de précaution ont également été prises pour éliminer les résultats non valides, en particulier, pour détecter le braconnage.

Les données enregistrées comprenaient la date, la station, le nombre de casiers valides, le nombre de homards capturés et le nombre de jours d'immersion de la ligne. Pour chaque homard, on notait la longueur du céphalothorax (CT), le stade de la mue et le sexe. Dans le cas des femelles, on notait, en plus, la présence ou l'absence d'oeufs. Pour les individus à marquer ou recapturés, on notait également le type et le numéro d'étiquette ou le code de poinçonnage. L'échantillonnage par casier s'est effectué à 8 stations dans la lagune de Grande-Entrée et à 11 stations dans celle de Havre-aux-Maisons au cours des deux saisons estivales 1978 et 1979 et, sur la côte, dans un secteur de moins de 10 km de l'embouchure du Havre-aux-Maisons entre le 28 juin et le 12 juillet 1978 (fig. 1).

Détermination des Stades de Mue

La détermination du stade de la mue s'effectuait à partir de l'examen de certaines caractéristiques macroscopiques de la carapace. Les homards en période de mue étaient ceux dont le mérus des pinces présentait une flexibilité légère ou marquée sous la pression des doigts. Selon Ennis (1973) le mérus est très flexible à partir de 3 jours avant l'exuviation, ce qui signifie que nous avons vraisemblablement déclaré en mue des homards dont l'exuviation pouvait se produire jusqu'à environ une semaine après la date d'observation. L'information sur une mue récente ($\leq$ 14 jours) était obtenue à partir du critère de la flexibilité du céphalothorax ("buckle shell," Templeman 1936) qui demeure enfonçable sous la pression des doigts pour une période d'environ 2 sem après l'exuviation. Une carapace datant de la saison précédente se distinguait facilement d'une première ou deuxième mue estivale par sa dureté, son éclat, sa couleur foncée, sa texture usée et rayée, de même que par la présence d'épizooïdes. La proportion de homards ayant effectué une première mue a été estimée par le pourcentage de nouvelles carapaces.

Méthodes de Marquage

Une première méthode de marquage consistait en la pose d'étiquettes sphyrion (subthoraciques) selon les techniques décrites par Scarratt (1970) et Cooper (1970). La deuxième méthode était celle des étiquettes de carapace qui sont perdues lors de la mue (Wilder 1953; Montreuil 1953; Bergeron 1967). Finalement, la troisième méthode consistait à utiliser un poinçon à cuir modifié pour perforer des trous de 2 à 3 mm sur les différentes pièces de l'urosome selon un code qui représentait la classe de taille du homard. Au moment de la recapture, une cicatrice recalcifiée et partiellement refermée indiquait qu'une mue avait eu lieu (Wilder 1953).

Méthodes de Capture

Les données de captures pour l'embouchure du havre de la Grande-Entrée en 1978 et 1979 nous ont été fournies par le

Centre de recherches écologiques de Montréal (Burton et al. 1980). Ces résultats proviennent de pêches de 10 lignes de 10 casiers mouillés entre le 28 septembre et le 10 novembre 1978 et de 13 lignes de 10 casiers entre le 1er mai et le 14 juillet 1979. Ces lignes de casiers étaient disposées de façon à couvrir entièrement le secteur de l'embouchure de la lagune du havre de la Grande-Entrée (fig. 1) et étaient relevées au moins une fois par 2 jours.

Les données sur la dispersion autour des Îles-de-la-Madeleine du homard marqué dans les lagunes en 1978 proviennent de la pêche commerciale effectuée entre le 10 mai et le 10 juillet 1979. En vertu d'un programme de prime à la recapture et grâce à la collaboration du ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec (MAPAQ), les données de recapture (no d'étiquettes, lieu et date de capture, longueur du céphalothorax, sexe, présence ou absence d'oeufs) ont été recueillies aux différents ports de débarquement, tout autour des Îles-de-la-Madeleine. La pêche commerciale couvrait toutes les côtes des Îles jusqu'à environ 30 km vers le large, mais non les lagunes qui ont un statut légal de sanctuaire.

Mesures de Température

La température de l'eau a été enregistrée de façon continue à une profondeur de 4 m dans le chenal à l'embouchure du Havre-aux-Maisons entre le 19 juin et le 6 août 1978 (Thermographe Yellow Spring Instrument), et entre le 20 mai et le 28 juin 1979 (Thermographe Ryan modèle J-90). Un enregistrement continu (Y.S.I.) a aussi été effectué à 1 m entre le 29 août et le 28 septembre 1978 dans le chenal à l'embouchure du havre de la Grande-Entrée. De ces enregistrements en continu, nous avons utilisé les moyennes journalières des températures à marée baissante puisque ce sont des températures qui se comparent le mieux aux températures lagunaires. Au cours des deux saisons d'échantillonnage, d'autres mesures ponctuelles de température ont également été effectuées à quatre profondeurs (0, 1, 3 et 4 m) aux diverses stations d'échantillonnage dans les deux lagunes. D'autres mesures ont occasionnellement été réalisées sur la côte adjacente aux deux lagunes durant la même période et ainsi qu'au cours de l'été 1981.

Résultats

En 1978, 3 335 homards furent capturés par casiers dans le Havre-aux-Maisons, 1 887 l'ont été sur la côte adjacente près de l'embouchure de cette lagune et 4 906 captures furent enregistrées pour le havre de la Grande-Entrée. En 1979, les captures dans le Havre-aux-Maisons représentent 2 368 homards. Au total, 12 496 homards furent capturés dont 6 752 furent marqués. Les recaptures représentent 1 373 homards, soit 20 %.

Différences de Température

Diverses mesures de température effectuées en surface et à 3 m dans les deux lagunes entre juin et novembre 1978 n'ont pas permis de déceler de différences significatives entre les profondeurs d'échantillonnage ($\overline{\Delta t} = 0.26$°C) ou entre les lagunes pour une même profondeur ($\overline{\Delta t} = 0.8$°C). Ceci permet de considérer les mesures provenant de l'une ou l'autre des lagunes comme étant des valeurs représentatives du milieu lagunaire. Par contre, des différences de température importantes ont été notées entre les eaux des lagunes et celles de la côte pour les mois de mai, juin, octobre et novembre (Δt variant entre 2 et 6°C). Entre juillet et septembre, les différences de température étaient faibles ($\Delta t < 2$°C) et souvent nulles. D'autres données ont mis en évidence la présence d'un gradient thermique important sur la côte adjacente à l'embouchure du Havre-aux-Maisons pour le mois de juin 1981 (fig. 2).

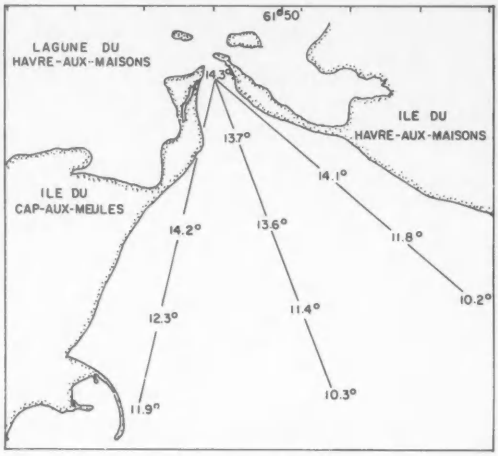

FIG. 2. Mesures de température (à 1 m) sur la côte adjacente à l'embouchure du Havre-aux-Maisons effectuées entre 16 et 18 h le 19 juin 1981.

Fluctuations Temporelles

Pour déterminer les périodes de migration du homard entre la côte et les lagunes et vice versa, nous avons comparé les fluctuations temporelles des pêches par unité d'effort (PUE) dans les deux lagunes et dans l'embouchure du havre de la Grande-Entrée avec celles de la température, des densités observées en plongée et de la proportion d'individus en mue pour les deux saisons d'échantillonnage 1978 et 1979 (fig. 3).

On note tout d'abord qu'avant le 15 mai et qu'après le 1er novembre les PUE sont à leurs plus bas niveaux autant dans les lagunes (fig. 3b) qu'à l'embouchure du havre de la Grande-Entrée (fig. 3c). En novembre, les densités moyennes observées en plongée (fig. 3e) sont presque nulles (moyenne de 30 individus·km^2) et diffèrent significativement (test de t à $P \leq 0.001$: Snedecor et Cochran 1967) des densités d'août et de septembre (moyenne de 1 730 individus·km^2).

À partir de la mi-mai, on note une montée importante des PUE dans la lagune du Havre-aux-Maisons et dans l'embouchure du havre de la Grande-Entrée qui coïncide avec une augmentation importante de la température de l'eau dans cette lagune. Vers la fin mai, les PUE se stabilisent à un faible

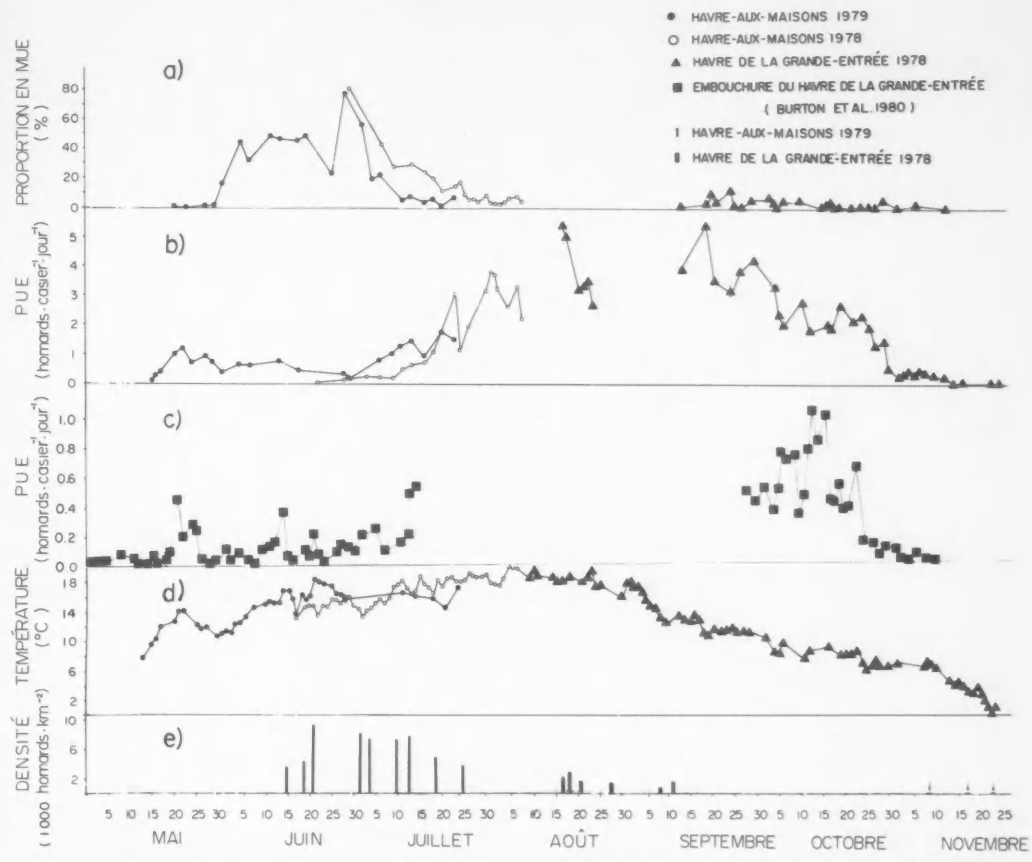

FIG. 3. Fluctuations temporelles de la proportion de homards en mue (a), des prises par unité d'effort dans les lagunes (b) et à l'embouchure du havre de la Grande-Entrée (c), de la température journalière moyenne de l'eau (d) et de l'indice d'abondance (densité) par plongée (e).

niveau dans la lagune en même temps qu'augmente la proportion de homards en mue. Le pourcentage de homards en mue demeure au niveau de 40 à 50 % pendant tout près d'un mois, ce qui suggère l'arrivée continuelle de nouveaux homards n'ayant pas encore mué dans les lagunes. Nous avons déterminé cette deuxième mue par notre indice de mue qui permet de déceler des différences de l'ordre de 1 semaine. Cette période importante de mue s'étend jusqu'au début juillet, soit le moment qui marque le début d'une remontée graduelle importante des PUE dans les lagunes. Cette augmentation des PUE correspond à une forte réduction du nombre de homards en mue, tandis que la température et les densités en plongée demeurent stables. On constate de plus qu'entre la mi-mai et le début juillet, les pics de PUE à l'embouchure de la lagune du havre de la Grande-Entrée correspondent en général à des périodes d'augmentation subite de la température de l'eau dans cette lagune. Ces pics de PUE pourraient refléter des mouvements d'entrée plus accentués du homard dans les lagunes.

À partir du début d'octobre, les PUE dans la lagune du havre de la Grande-Entrée diminuent graduellement en même temps qu'augmentent les PUE dans la région de l'embouchure. Vers la fin octobre, on note une diminution brusque des PUE dans ces deux endroits. En ce qui concerne la température, il y a diminution plus ou moins graduelle à partir du début septembre. Ces résultats suggèrent une sortie massive du homard de la lagune du havre de la Grande-Entrée entre le début octobre et le début novembre.

LA MUE DANS LES LAGUNES

La figure 3 montre qu'une proportion importante de la population de homard lagunaire est en mue entre le début juin et la mi-juillet. Ce pourcentage de homards en mue atteint plus de 75 % des captures vers la fin juin. Il semble cependant qu'en 1979 la mue ait eu lieu quelque 10 jours plus tôt qu'en

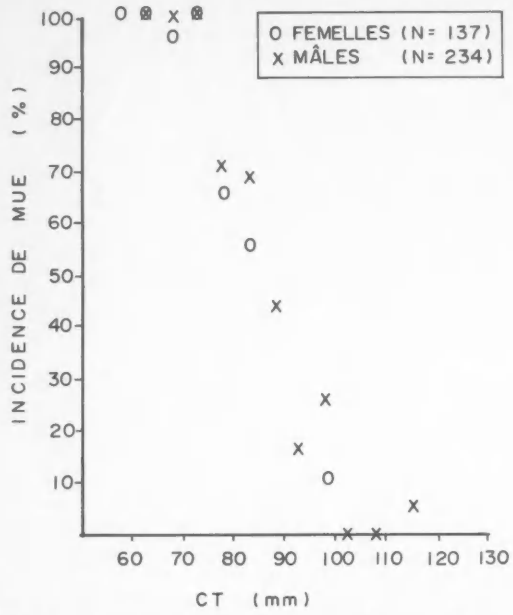

FIG. 4. Pourcentage de homards mâles et femelles ayant subi une deuxième mue en fonction de la taille des individus capturés dans les deux lagunes du Havre-aux-Maisons et du havre de la Grande-Entrée.

1978 si l'on en juge par une réduction plus précoce de la proportion de homards en mue en 1979. Suivant cette période de mue, le pourcentage de carapaces neuves dans nos échantillonnages nous a permis d'estimer à environ 95 à 97 % la proportion de homards qui ont effectué au moins une mue dans les lagunes en 1978 et 1979.

Par ailleurs, il est intéressant de noter que de septembre jusqu'à la mi-novembre, on observe encore des proportions de 1 à 10 % des homards en mue dans le havre de la Grande-Entrée en 1978. Les recaptures à la pêche commerciale en 1979, des homards marqués dans les lagunes après la première mue en 1978, ont révélé une forte incidence de mue même si elles ont été effectuées avant la première période de mue (avant la mi-mai). Nous en concluons donc à l'existence d'une deuxième période de mue dans les lagunes. Les taux résiduels de homards en mue observés à partir de septembre représenteraient la fin de cette deuxième période de mue. En se référant à la baisse prononcée des PUE dans le havre de la Grande-Entrée entre le 17 et le 24 août (fig. 3b) qui pourrait refléter l'inactivité caractéristique du homard en période de mue, nous situons approximativement cette période de deuxième mue entre le 15 août et le 15 septembre.

L'examen des résultats de marquage en période post-1re mue dans les lagunes en 1978 et de recaptures à la pêche commerciale en 1979 en période pré-1re mue nous permet de constater que 100 % des mâles de moins de 75 mm de longueur CT ont subi au moins deux mues dans les lagunes (fig. 4). Ce pourcentage diminue rapidement en fonction de la taille pour atteindre moins de 5 % pour des tailles de plus de 105 mm. Le femelles montrent des pourcentages de deuxième mue semblables, excepté que 98 mm représente la limite supérieure de l'échantillonnage.

À partir de la recapture de 34 mâles et de 33 femelles marqués au sphyrion, nous avons pu estimer la croissance en longueur du céphalothorax consécutive à une mue dans les lagunes. Les deux équations reliant la longueur post-exuviale (y) à la longueur pré-exuviale (x) chez les mâles et les femelles sont les suivantes :

$$(1)\quad \text{(mâles)} \quad y = 1.00x + 11.35 \qquad (r = 0.97)$$

$$(2)\quad \text{(femelles)} \quad y = 1.10x + 2.22 \qquad (r = 0.94).$$

Les deux coefficients de régression sont significatifs à $P \leq 0.01$.

Donc, pour notre échantillonnage de mâles de longueur CT variant entre 63 et 112 mm, on a calculé un accroissement de longueur de 11,3 mm par mue, soit 14 % de la longueur pré-exuviale moyenne (83 mm). Pour les femelles (CT variant entre 66 et 82 mm) le gain en longueur est de 9,5 mm, soit 13 % de la longueur pré-exuviale moyenne (73 mm).

STRUCTURE DE TAILLE

Les figures 5 à 7 présentent les distributions des fréquences de taille pour divers échantillonnages par casier réalisés dans le Havre-aux-Maisons en 1978 (fig. 5) et en 1979 (fig. 6), dans le havre de la Grande-Entrée en 1978 (fig. 7b) et dans la région côtière adjacente à Grande-Entrée en 1978 (fig. 7a). Ces échantillonnages ont été choisis comme étant représentatifs de la structure de taille durant les périodes de pré-1re mue, post-1re mue ou de post-2e mue. L'objectif poursuivi est de pouvoir comparer les structures de population entre les deux lagunes, entre les lagunes et la côte, ou encore entre deux périodes différentes pour la même lagune.

Une façon d'effectuer ces comparaisons est de prendre un histogramme de taille pour une période pré-mue et de le corriger pour la mue en utilisant pour chaque classe de taille au-dessus de 70 mm de longueur CT une incidence de 100 % dans le cas d'une 1re mue et les résultats de la figure 4 pour une 2e mue. On applique ensuite les équations (1) et (2) pour les accroissements en longueur par mue. Le total cumulatif des nouvelles fréquences obtenues est ensuite pondéré au total cumulatif des fréquences de l'histogramme post-mue utilisé pour la comparaison. Les nouvelles structures de taille ansi corrigées pour la mue pour les classes admissibles sont ensuite comparées aux histogrammes post-mue correspondants. Ces comparaisons sont présentées sur les figures 5 à 7, où les histogrammes corrigés d'une période pré-mue (points noirs sur les histogrammes) sont superposés aux structures de taille post-mue correspondantes. Le test de Kolmogorov–Smirnov (Siegel 1956) a ensuite été utilisé pour évaluer la ressemblance entre les histogrammes comparés.

Les résultats de ce test n'indiquent pas de différence significative (à $P \leq 0.05$) entre les structures de taille pré-mue et post-mue du Havre-aux-Maisons (fig. 5 et 6) dans tous les cas, qu'il s'agisse des mâles ou des femelles si l'on tient compte de la mue. La structure de la population est donc

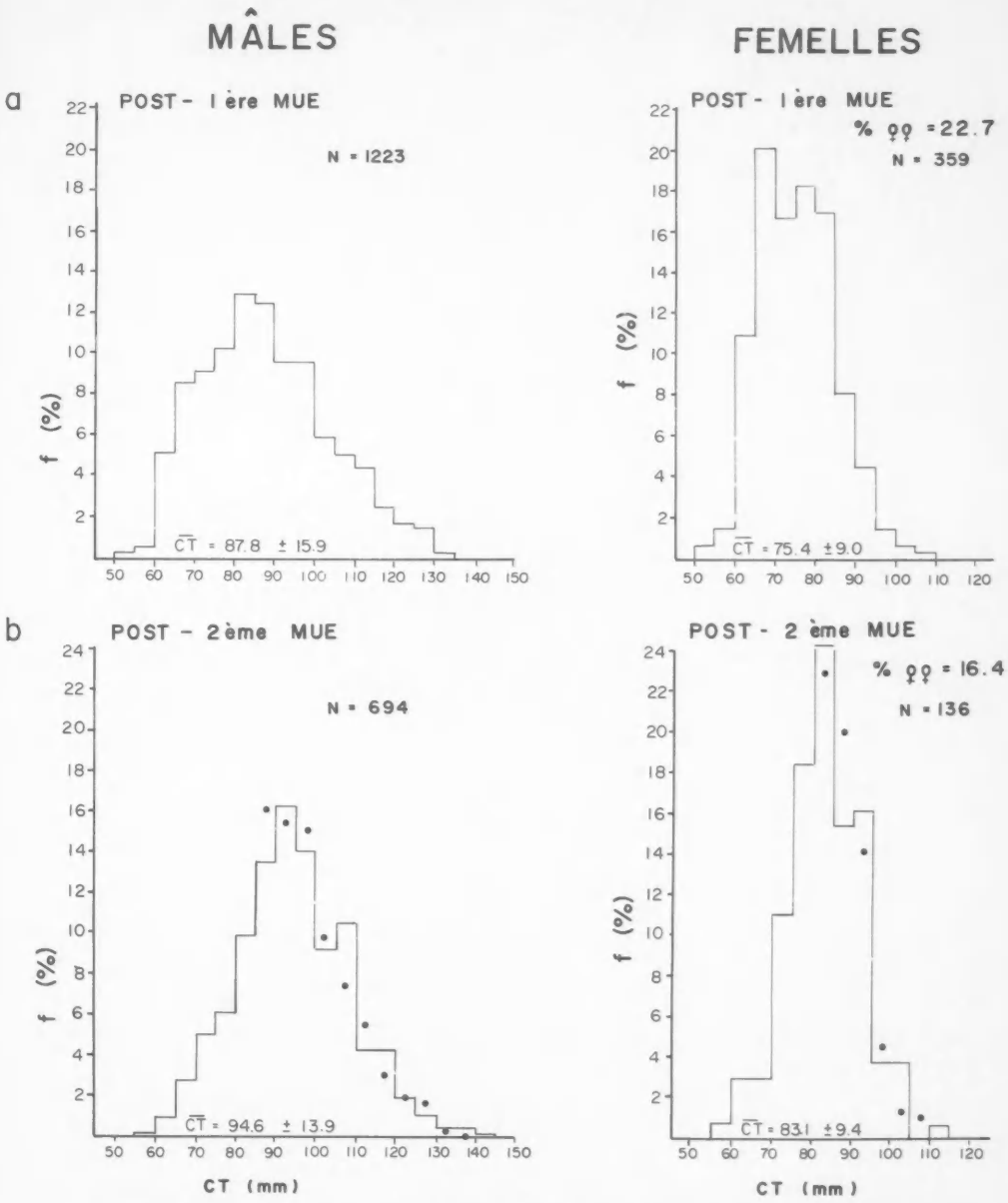

FIG. 5. Distribution des fréquences de tailles des homards mâles et femelles en périodes post-1re mue (a) et post-2e mue (b) pour le Havre-aux-Maisons et 1978. Les points sur les histogrammes représentent la distribution des fréquences estimée à partir de l'échantillonnage pré-mue correspondant (voir le texte pour plus de détails).

demeurée inchangée dans la lagune du Havre-aux-Maisons pour les différentes périodes de l'année entre la période d'entrée et celle de sortie. On note toutefois que le pourcentage de femelles diminue, suite à la mue, au cours des deux saisons

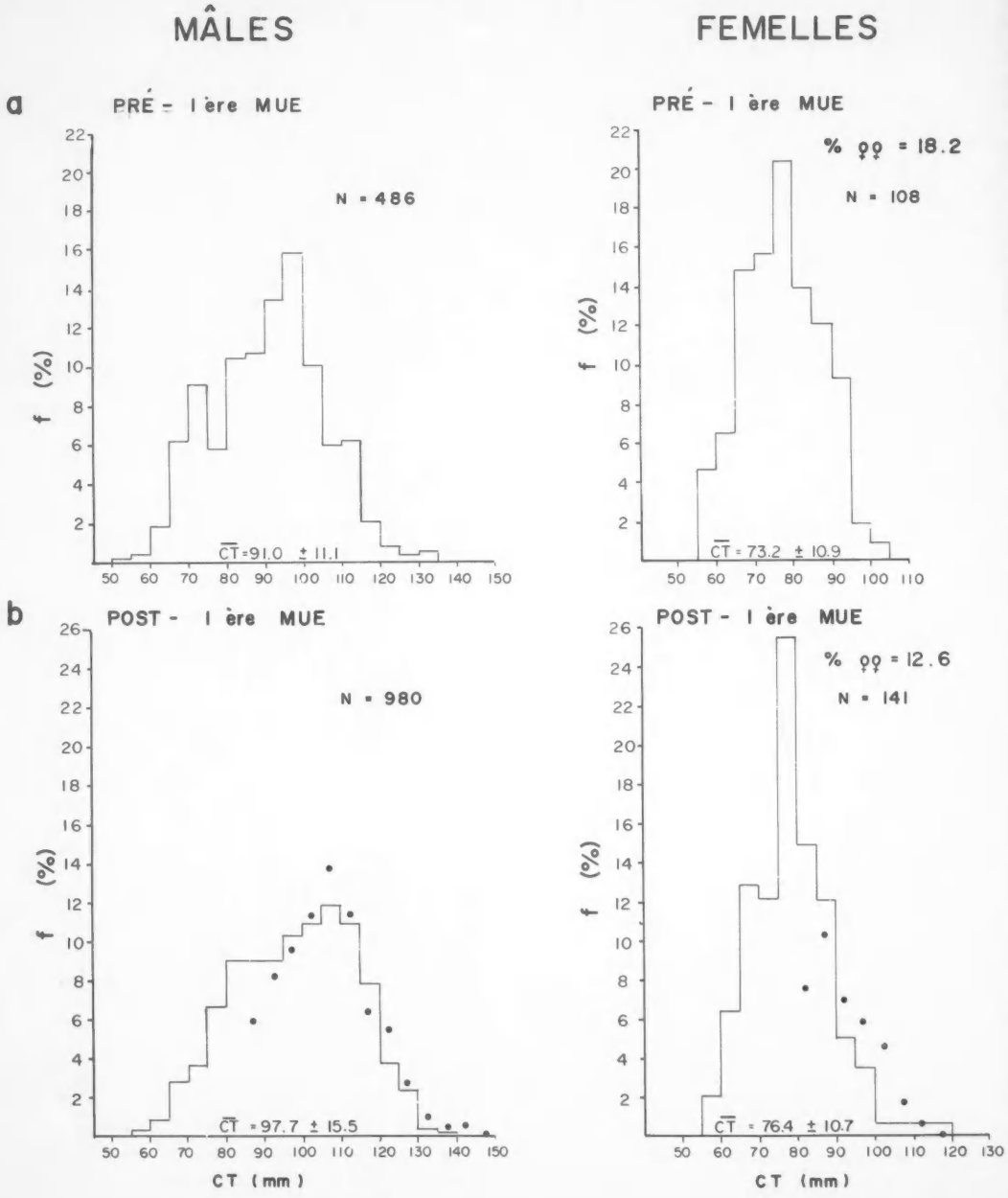

FIG. 6. Distribution des fréquences de tailles de homards mâles et femelles en période pré-1re mue (a) et post-1re (b) pour le Havre-aux-Maisons en 1979.

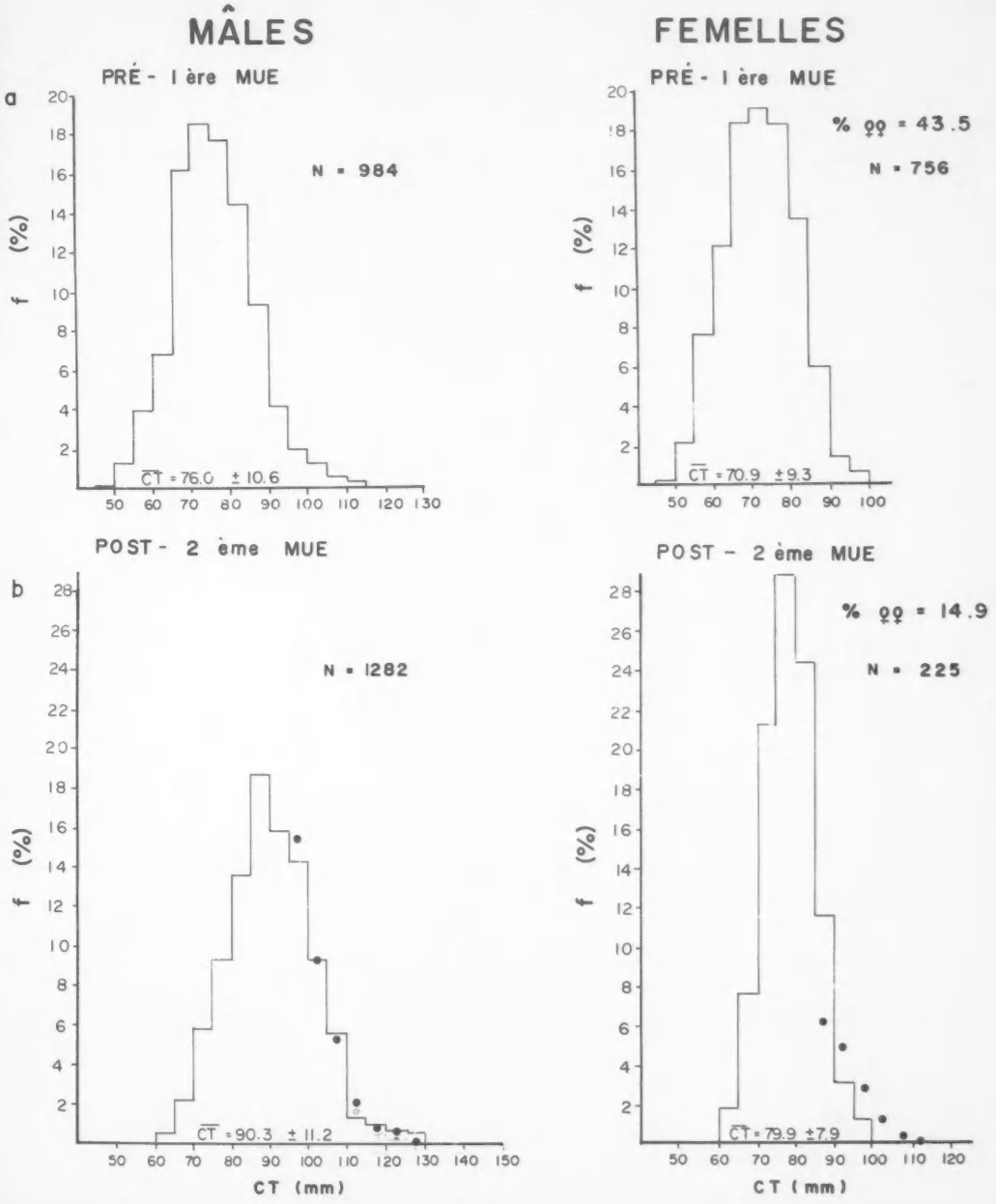

FIG. 7. Distribution des fréquences de tailles de homards mâles et femelles en période pré-1re mue (a) pour les captures côtières en 1978 (Anonyme 1978) et en période de post-2e mue (b) pour le havre de la Grande-Entrée en 1978.

FIG. 8. Localisation des recaptures à la pêche commerciale en 1979 du homard marqué en 1978 dans le havre de la Grande-Entrée (a), dans le Havre-aux-Maisons (b) et sur la côte en face de Havre-aux-Maisons (c).

de 1978 et 1979 (fig. 5 et 6). Cette diminution peut s'expliquer par le fait qu'à la mue, une proportion plus faible de femelles atteindrait la longueur CT de 70 mm, taille à partir de laquelle le taux de rétention des casiers est de 100 % pour en espacement de lattes de 34 mm (Krouse et Thomas 1975). Nos données de plongées pour le Havre-aux-Maisons en 1979 ont d'ailleurs montré que pour les tailles de moins de 70 mm, la longueur moyenne des femelles ($N = 24$) était de 6 mm inférieure à celles des mâles ($N = 76$). Il y aurait donc des chances qu'à la mue une plus grande proportion de mâles que de femelles atteignent les longueurs plus facilement capturables par casier. De plus, l'accroissement en longueur par mue est généralement inférieur chez les femelles qui approchent la taille de la maturité telle que déterminée par la taille minimale des femelles ovigères observées (de 55 à 65 mm dans les lagunes). Finalement, on remarque qu'entre les deux années 1978 et 1979, les structures de taille pour la même période post-1re mue dans la lagune du Havre-aux-Maisons sont significativement différentes (fig. 5a et 6b). Les mâles sont beaucoup plus gros en 1979 (CT = 98 mm) qu'en 1978 (CT = 88 mm), mais non les femelles. Par contre, les femelles ne représentent que 13 % de la population en 1979 comparé à 23 % en 1978.

La comparaison (Kolmogorov−Smirnov) entre les deux lagunes pour une même période post-2e mue 1978 (fig. 5b et 7b) indique une plus forte abondance relative de homards de grande taille dans le Havre-aux-Maisons. Ceci s'applique autant aux mâles qu'aux femelles ($P \leq 0.01$).

Pour comparer la population de homard lagunaire à la population côtière, nous avons utilisé les résultats d'un échantillonnage (fig. 7a) réalisé en période pré-1re mue à moins de 10 km au large du havre de la Grande-Entrée (Anonyme 1978). Nous avons simulé une 1re et 2e mue sur cet échantillonnage et l'avons comparée à la structure de taille post-2e mue pour le havre de la Grande-Entrée en 1978 (fig. 7b). La comparaison indique une structure de taille semblable pour les mâles, mais significativement différente pour les femelles (Kolmogorov−Smirnov, à $P \leq 0.01$). Ce ré-

TABLEAU 1. Comparaison entre le nombre de marques posées (M), le nombre de recaptures (R) et le taux de retour (T) pour l'ensemble des échantillonnages effectués dans les lagunes en 1978 et 1979 et à la pêche commerciale en 1979 (a) et pour un marquage dans la lagune du Havre-aux-Maisons en 1978 et une recapture en 1979 dans la même lagune (b). Seuls les homards de plus de 70 mm de longueur CT sont considérés dans ce tableau. NS, une différence non significative entre le retour des mâles et des femelles; *, un pourcentage de retour significativement différent (test de χ^2 à $P \leq 0.05$) entre les mâles et les femelles.

Marquage	Recapture		M	R	T (%)	
(a) Havre de la Grande-Entrée et Havre-aux-Maisons en 1978	Havre de la Grande-Entrée et Havre-aux-Maisons en 1978 et pêche commerciale en 1979	Mâles	5 578	559	10,0	NS
		Femelles	959	84	8,8	
(b) Havre-aux-Maisons en 1978	Havre-aux-Maisons en 1979	Mâles	1 558	78	4,8	*
		Femelles	340	5	1,5	

sultat suggère une différence entre les migrations des mâles et des femelles.

Pour le Havre-aux-Maisons les tailles moyennes des mâles en période pré-1re mue en 1978 (81 mm) et en 1979 (91 mm) sont nettement supérieures aux tailles moyennes observées sur la côte adjacente (76 mm : Bergeron 1967; Axelsen et Dubé 1978). Une telle différence n'existe pas entre les tailles des femelles côtières et lagunaires. Les femelles sont beaucoup plus abondantes dans l'échantillonnage côtier (44 %) que dans les lagunes (13 à 23 %). En ne considérant que les tailles commerciales, la proportion de femelles est de 37 % pour la côte et de 9 % en moyenne pour les lagunes. Par contre les femelles ovigères représentent 13 à 16 % des femelles capturées en période pré-1re mue dans les lagunes et seulement 7 % dans l'échantillonnage côtier (Anonyme 1978).

DISPERSION CÔTIÈRE ET RETOUR AUX LAGUNES

La dispersion du homard sur la côte adjacente suivant sa migration hors des lagunes a été étudiée à partir des recaptures durant la pêche commerciale en 1979. Des 349 recaptures d'individus qui avaient été marqués dans le havre de la Grande-Entrée (fig. 8a), 67 % proviennent de moins de 5 km de la côte entre Old-Harry et l'Ile Shag. Des 77 recaptures d'individus marqués dans la lagune du Havre-aux-Maisons (fig. 8b), 75 % proviennent de la région située entre l'Ile Shag et Gros-Cap, à moins de 3 km de la côte. Finalement, des 954 individus marqués sur la côte en face de Havre-aux-Maisons (fig. 8c), 75 % des recaptures se distribuent à moins de 3 km de la côte, en direction de Grande-Entrée. De façon globale, on peut dire que 98 % de toutes les recaptures ont été effectuées entre Old-Harry et Gros-Cap, à l'intérieur d'une bande de 30 km de largeur le long de la côte sud-est des Iles. Les recaptures ont été plus nombreuses vers le nord-est que vers le sud-est, ce qui pourrait signifier un déplacement en général vers le nord-est. La proportion de recaptures effectuées à moins de 10 km de l'embouchure de la lagune d'origine est de 71 % dans le cas du Havre-aux-Maisons et de seulement 37 % dans celui de la Grande-Entrée. Il est finalement intéressant de noter que des 954 homards marqués sur la côte entre le 28 juin et le 12 juillet 1978, aucun n'a été recapturé par la suite à l'intérieur de la lagune du Havre-aux-Maisons en 1978. De plus, pour cette même année, aucune recapture de homards marqués dans le Havre-aux-Maisons n'a été effectuée dans le havre de la Grande-Entrée et vice versa.

Pour le Havre-aux-Maisons, on a également estimé un taux de retour à la lagune suivant la sortie automnale 1978 en utilisant les données de marquage au poinçon dans la lagune en 1978 et de recapture en 1979 (tableau 1b). Ce taux de retour T est calculé de la façon suivante :

$$(3) \quad T = \frac{\hat{M}_{79}}{M_{78}}$$

où M_{78} représente le nombre d'individus marqués au poinçon dans la lagune en 1978 et $\hat{M}_{79}$ représente une estimation du nombre de homards marqués de retour dans la lagune en 1979. On estime $\hat{M}_{79}$ par

$$(4) \quad \hat{M}_{79} = \frac{\hat{N}_{79} R_{79}}{C_{79}}$$

où $\hat{N}_{79}$ représente l'estimation de la population lagunaire obtenue par plongée (Munro et Therriault 1981), R_{79} est le nombre de recaptures et C_{79} le nombre total de homards capturés en 1979 dans la lagune. Pour pouvoir faires des comparaisons avec la pêche commerciale de 1979, seules les tailles $\geq$ à 76 mm de longueur CT ont été utilisées dans nos estimations du taux de retour. Nous avons ainsi pu estimer que 64 % des mâles et 22 % des femelles retournaient à la lagune, ce qui donne un taux de retour moyen de 55 % avec un coefficient de variation de 36 %. Les données de recapture dans le Havre-aux-Maisons en 1979, du homard marqué dans cette même lagune en 1978 indiquent également un taux de retour à la lagune significativement plus faible (test de χ^2 à $P \leq 0.05$) pour les femelles que pour les mâles (tableau 1b). Il ne semble pas que ce résultat puisse s'expliquer par un biais dans la méthode d'échantillonnage puisque nous n'avons pas noté de différences significatives entre les taux de retour des mâles et des femelles dans notre échantillonnage (tableau 1a). Par ailleurs, les données de recaptures dans le havre de la Grande-Entrée de homards marqués sur la côte (Anonyme 1978) indiquent une zone côtière de recrutement d'environ 15 km autour de l'embouchure de cette lagune.

Discussion et conclusion

Il est reconnu que l'indice de capture PUE dépend de trois facteurs principaux soit la densité, le stade de mue et la température. La mue est précédée d'une période d'inactivité

d'une semaine ou plus et elle est suivie, après quelques jours, d'une forte recrudescence d'activité (Stewart 1972; Weiss 1970). La capturabilité est positivement corrélée avec la température (McLeese et Wilder 1958; Paloheimo 1963). Enfin, les captures devraient aussi varier proportionnellement à la densité de homards présents dans les lagunes. Cette dépendance des PUE sur ces trois facteurs peut nous aider à comprendre les résultats que nous avons obtenus. En effet, les très faibles prises du début et de la fin de saison (fig. 3) ne peuvent s'expliquer que par une très faible densité ou une absence du homard dans les lagunes. Cette hypothèse est confirmée par les plongées de la fin novembre qui indiquent l'absence de homards, de tunnels ou de monticules d'enfouissement sur les transects de plongée : ce qui exclut en même temps que les basses températures aient pu être responsables des moins bonnes prises en favorisant une inactivité du homard. Par ailleurs, les captures presque nulles obtenues au début de mai à l'embouchure de la lagune de la Grande-Entrée (fig. 3c) indiquent également une absence de homards dans les lagunes pour le début du printemps. La faible densité de homards durant ces deux périodes pourrait être liée à la présence de températures de moins de 10 à 11°C dans les lagunes. Aussitôt que la température de l'eau augmente au printemps à plus de 11°C, on note une augmentation des prises qui ne peut s'expliquer que par une mouvée ou entrée du homard dans les lagunes. Cette entrée du homard peut s'étendre vraisemblablement jusqu'à la fin juin-début juillet comme le suggèrent les résultats obtenus à l'embouchure du havre de la Grande-Entrée (fig. 3b). De même, lorsque la température descend à moins de 11°C vers la fin octobre, on observe une baisse rapide des PUE qui s'explique par une sortie du homard des lagunes. Ce mouvement de sortie coïncide avec la diminution des captures à l'embouchure du chenal du havre de la Grande-Entrée (fig. 3e).

Nos résultats confirment donc l'existence de migrations actives du homard entre la côte et les lagunes aux Îles-de-la-Madeleine. Ces entrées (de la mi-mai à la fin juin) et sorties (du début à la fin octobre) saisonnières du homard dans les lagunes coïncident avec le réchauffement et le refroidissement de la colonne d'eau et sont vraisemblablement partie intégrante d'un phénomène plus général de migrations saisonnières liées à la température de l'eau, et propre à certains milieux côtiers (Templeman 1936; Corrivault 1948; Montreuil 1960; Bergeron 1967; Jeffries et Johnson 1974; Uzmann et al. 1977; Anonyme 1978).

Les travaux de McLeese (1956, 1958, 1972) et de McLeese et Wilder (1958) suggèrent qu'il pourrait exister une température optimale recherchée par le homard, température qui se situerait aux alentours de 15°C. Ces travaux ont aussi démontré que le homard réagirait à des augmentations de température de l'ordre de 2 à 5°C par une activité accrue pour les homards acclimatés à des températures inférieures à 15°C et par une activité inchangée ou réduite pour des homards acclimatés à plus de 15°C. D'après nos résultats de tels écarts de température sont fréquents entre les lagunes et le milieu côtier adjacent pendant les périodes de migration du printemps (mai et juin) et de l'automne (octobre et novembre), et sont véhiculés par la marée jusqu'à au moins 4 km de l'embouchure des lagunes (fig. 2). Il y aurait ainsi la suggestion d'une relation de cause à effet entre les mouvements d'entrée accentués du homard observés à l'embouchure du havre de la Grande-Entrée (fig. 2) et les augmentations subites et coïncidentes de la température dans les lagunes. Le homard serait donc capable de détecter des gradients de température et pourrait alors essayer de se maintenir dans des masses d'eau entre 10 et 20°C. Les migrations du homard seraient ainsi liées aux déplacements saisonniers des isothermes de 8 à 11°C tant dans les lagunes que sur la côte. L'absence de gradients de température pourrait expliquer le fait que certains milieux côtiers (Cooper et al. 1975; Wilder et Murray 1958) ne montrent pas de mouvement migratoire du homard, à moins que le patron d'échantillonnage n'ait pas permis de détecter de telles migrations. De même peut-on penser que l'arrêt des échanges entre la côte et les lagunes à partir de juillet pourrait être dû à l'absence de gradient important de la température entre les lagunes et la côte à partir de cette période jusqu'à octobre.

Suite à sa sortie des lagunes, le homard montre une dispersion parallèle à la côte avec une tendance vers la direction nord-est, tout en demeurant à proximité de son lieu de marquage. Ces résultats sont en accord avec ceux de Templeman (1935), Montreuil (1960), Bergeron (1967) et Belzile et Fréchette (1980). En considérant la topographie locale des Îles-de-la-Madeleine et le fait que les données actuellement disponibles (El-Sabh 1976) suggèrent une direction dominante des courants vers le sud-ouest sur la côte sud des Iles, cette tendance pourrait s'expliquer pour un organisme marin qui doit compter principalement sur des stimuli chimiques pour reconnaître son environnement (McLeese 1973). Le homard devant se déplacer le plus souvent à contre-courant, on doit s'attendre statistiquement à une tendance nord-est dans sa dispersion sur la côte des Îles-de-la-Madeleine, si effectivement un courant en direction sud-ouest est dominant sur le fond. D'autre part, certains auteurs (Stasko 1978; Dadswell 1979) prétendent que la tendance à une dispersion à contre courant provient d'une adaptation qui aurait pour but de favoriser le recrutement sur les fonds propices à la croissance par le relâchement des larves à l'avant du courant moyen.

Nos données indiquent qu'une grande proportion du homard subirait deux mues dans les lagunes. Ces résultats confirment et précisent les travaux antérieurs de Templeman (1935, 1936) montrant que pour la baie de Malpèque et les lagunes des Îles-de-la-Madeleine, le petit homard ($\leq$ 80 mm) subissait deux mues et que la première mue avait lieu dans ces endroits 2 sem à un mois plus tôt que sur les côtes adjacentes. Tout comme Templeman (1936), nous croyons que les différences de température entre les masses d'eau sont à l'origine de ce phénomène. Des fréquences de deuxième mue telles que celle que nous avons trouvée pour les lagunes ont également été observées pour les eaux plus chaudes du détroit de Northumberland (Templeman 1935, 1936; Wilder 1963). Par ailleurs, il ne semble pas y avoir de 2e mue sur la côte sud des Îles-de-la-Madeleine (P. Dubé, MAPAQ, communication personnelle) pour les homards de taille commerciale.

En tenant compte des deux périodes de mue, nous avons pu effectuer des comparaisons valides entre les différentes populations pour une même période ou encore entre des périodes différentes pour une même population. La stabilité temporelle de la structure de taille des populations lagunaires confirme l'arrêt ou la restriction des échanges entre les lagunes et la

côte en période estivale. Comme on l'a vu, l'absence de gradients thermiques importants de juillet jusqu'à octobre pourrait expliquer cette restriction. Considérant qu'au cours de la même période, les populations des deux lagunes ont une structure de taille différente, on en conclut, comme avec les résultats de marquage/recapture, qu'il y a peu ou pas d'échanges directs entre les deux lagunes et que ces deux populations sont distinctes même si leur évolution temporelle apparaît parallèle selon les données des PUE (fig. 3).

On a constaté que dans les lagunes, le pourcentage de mâles est de beaucoup supérieur à celui de la côte (Anonyme 1978; Axelsen et Dubé 1978; Bergeron 1967). Il nous est difficile d'expliquer ce résultat si ce n'est en postulant l'existence d'une sélection positive en faveur de la mobilité des mâles lors des périodes de migrations de la côte vers les lagunes. L'hypothèse d'une mobilité différente en fonction de la taille, du sexe ou de l'état de maturité, ou encore celle d'une recherche plus active de conditions particulières (température, habitat, etc.) pour les mâles que pour les femelles restent à examiner pour expliquer cette sélectivité.

On a aussi noté, pour le Havre-aux-Maisons, que les tailles moyennes des mâles étaient plus grandes que sur la côte. La simple observation d'un retour annuel très élevé à la lagune pour les mâles doit résulter en une taille moyenne plus grande dans les lagunes que sur la côte, puisqu'un fort pourcentage de ces mâles ont connu dans les lagunes une croissance plus grande (deux mues) que les mâles de la population côtière. Ceci pourrait également expliquer les différences de tailles observées chez les mâles entre les deux saisons estivales 1978 et 1979. En effet, en raison d'un réchauffement hâtif des eaux et, par conséquent, d'une migration plus précoce en 1979, il est possible qu'un plus grand nombre de gros individus aient échappé à la pêche commerciale de 1979 comparé à celle de 1978, en pénétrant dans les lagunes avant que la pêche commerciale ne débute. Par contre, on a observé des structures de tailles semblables entre la lagune de Grande-Entrée et la côte pour les mâles. Ces différences pourraient s'expliquer par des exploitations plus grandes du homard par la pêche commerciale dans la région côtière adjacente à Grande-Entrée que dans celle adjacente à Havre-aux-Maisons tel que suggéré par le pourcentage de recaptures côtières significativement plus élevé (test de χ^2 à $P \leq 0.05$) pour la zone côtière de Grande-Entrée (26 %) que pour celle du Havre-aux-Maisons (19 %). Il y a aussi le fait qu'à la sortie des lagunes, le homard du Havre-aux-Maisons semble se disperser dans une région moins vaste que celui de Grande-Entrée (fig. 8). Le gros homard du Havre-aux-Maisons aurait donc plus de chances d'éviter la pêche commerciale que celui de Grande-Entrée. Finalement, on pourrait également attribuer à la pêche commerciale les pourcentages plus élevés de femelles ovigères dans les lagunes que sur la côte puisque les femelles ovigères ne sont pas exploitées par cette pêche au cours de la période de migration dans les lagunes.

Nos résultats nous permettent donc de conclure à l'existence de migrations saisonnières du homard lagunaire des Iles-de-la-Madeleine qui seraient reliées à des variations de la température des masses d'eau. Lors de la migration printanière dans les lagunes, il s'exercerait une sélectivité en faveur de la mobilité des mâles, mais les différences dans les tailles moyennes seraient dues à la pêche commerciale. Celle-ci contribuerait également à biaiser les pourcentages de femelles ovigères entre la côte et les lagunes.

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Population Dynamics and Management of the Northwest Atlantic Harp Seal *(Phoca groenlandica)*

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Previous methods of estimating population size and natural mortality rate in harp seals (*Phoca groenlandica*) are reviewed. Excepting the method of Beddington and Williams (Marine Mammal Comm., Washington, DC., Rep. MMC 79-03, 1980) all previous methods rely heavily upon the survival index method of estimating pup production. We describe the mathematical rationale underlying this method and indicate potential sources of bias. Beddington and Williams' analysis produces a combination of vital rates for 1952 that would not enable a population to persist in the absence of hunting. This suggests that the method may not be able to estimate these parameters accurately. This conclusion is supported by several unpublished analyses. We present an alternative method of analysis that is based on the concept of maximum likelihood. We estimate the rate of natural mortality and trend in 1+ population size from 1967 to 1980, using mark–recapture estimates of pup production in the late 1970s and the observed ratio of the survival of adjacent cohorts in the late 1960s and early 1970s to constrain population trajectories from a simulation model. From this analysis we conclude that the population is increasing and that the present total catch may be substantially smaller than the replacement yield.

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Nous passons en revue les diverses méthodes utilisées dans le passé pour estimer les effectifs de population et les taux de mortalité naturelle du phoque du Groenland (*Phoca groenlandica*). Sauf celle de Beddington et Williams (Marine Mammal Comm., Washington, DC., Rep. MMC 79-03, 1980), toutes les autres méthodes dépendent étroitement de l'estimation de production des chiots à partir de l'indice de survie. Nous décrivons le fondement methématique de cette méthode et indiquons des sources potentielles de biais. L'analyse de Beddington et Williams donne une combinaison de taux de survie en 1952 qui ne permettrait pas à une population de se maintenir en l'absence de chasse. Ceci donne à penser que la méthode ne peut estimer ces paramètres avec précision. Plusieurs analyses inédites appuient cette conclusion. Nous présentons ici une alternative, fondée sur le concept de probabilité maximale. Nous estimons le taux de mortalité naturelle et la tendance des effectifs de population à l'âge 1+ entre 1967 et 1980. Nous utilisons pour cela les estimations de production de chiots par marquage et recapture à la fin des années 1970 et le rapport de la survie de cohortes adjacentes à la fin des années 1960 et au début des années 1970 afin de modérer les trajectoires de population découlant d'un modèle de simulation. Nous concluons, à la suite de cette analyse, que la population est en voie d'augmentation et que la récolte totale actuelle est peut-être substantiellement inférieure au rendement de remplacement.

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THE management of northwest Atlantic harp seals, *Phoca groenlandica*, has in recent years been the subject of controversy within both the scientific and popular literature. Much of this controversy concerns the present status of the population and future management policy. Recent assessments of fluctuations in population size from 1952 to the present (Lett and Benjaminsen 1977; Lett et al. 1979; Winters 1978) have

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been based largely on cohort analysis and a method of estimating pup production from catch-at-age information termed the survival index method (Sergeant 1975; Benjaminsen and Øritsland 1975). Estimates of past and present population are in close agreement, Lett and Benjaminsen (1977) estimating the 1977 population size of animals 1 yr and older (1+) to be 1.2 million, whereas Lett et al. (1979) and Winters (1978) both estimate it at 1.3 million. As there is considerable overlap in methodology employed, this agreement is not surprising. For this reason it is also not surprising that all three papers estimate the natural mortality rate of 1+ seals to be ~0.1. This rate is quite reasonable for a species living to age 30 or more and has been generally accepted. These analyses indicate that under the present catch quota the population should be increasing.

At a recent meeting sponsored by the World Wildlife Fund to examine the biology and management of the northwest Atlantic harp seal population, Beddington and Williams (1980) presented an alternate method of analyzing the historical data. By this method they estimate the natural mortality rate to be 0.1375. The analysis by Beddington and Williams (1980) also produces a different historical population trajectory, although by chance their estimate of the 1969 population size coincides with that derived using cohort analysis. Future projections of population size are significantly affected by the cumulative effect of this higher estimate of natural mortality rate. Their analysis suggests that the reduction in the level of kill, brought about by the first catch quota in 1971, did not halt the decline in the seal population, and that under the present quota the population will continue to decline. A closer examination of harp seal population dynamics is clearly warranted.

In this paper we examine the methods previously used to analyze harp seal population dynamics. We then present a new method that makes use of harp seal pup production estimates from recent mark–recapture experiments (Bowen and Sergeant 1983).

The Population

The following account of the biology of the northwest Atlantic harp seal is based largely on Sergeant (1976a). Harp seals are highly migratory marine mammals inhabiting Arctic waters in summer and subarctic waters around Newfoundland in winter. They begin their southward migration in late September when new arctic ice is forming, and by December the first migrants have reached northern Newfoundland. Here the population separates; about one third of the mature seals enter the Gulf of St. Lawrence to breed near the Magdalen Islands (known as the 'Gulf' herd) and the remainder continue down the east coast of Newfoundland and eventually breed on southward drifting arctic ice off southern Labrador (known as the 'Front' herd). During winter most immature harp seals feed in the 'Front' area, although some do migrate into the northern Gulf of St. Lawrence.

Females give birth to a single pup several days after they have hauled out onto the ice, with most births occurring over a 1-wk period beginning in late February in the Gulf and about March 8 at the Front. Newborn pups are covered with a long white fur from which they derive the name 'whitecoats.' Pups are nursed for about 9 d and then are abandoned by their mothers (Stewart and Lavigne 1980). Once abandoned, whitecoats at the Front continue to drift southward to rich feeding grounds in White and Notre Dame bays, Newfoundland. They also begin to shed their white fur at this time and after about 18 d of age this coat is completely shed and is replaced with the spotted juvenile pelage. Molted pups are known as 'beaters.'

As soon as females have finished lactation in March, but before they leave the whelping area, they are courted by males which have been waiting nearby in large herds. Mating appears to be promiscuous.

In early April harp seals haul out onto the receding pack ice usually east of Belle Isle to molt. Adult males and immatures, known as 'bedlamers,' molt first, followed by adult females which begin to molt about the 3rd week of April. After molting, harp seals age one and older migrate north. Beaters begin their northern migration in May and some reach West Greenland by early June. At this time adults and immatures are fairly well segrated with mature seals feeding mainly in the Canadian Arctic and the bedlamers and beaters inhabiting the waters off West Greenland.

Cohort Analysis and the Estimation of Natural Mortality

Cohort analysis (Pope 1972) is potentially a powerful tool for estimating changes in population size where catch-at-age data are available for a long sequence of years. A major problem with cohort analysis is that it depends upon an estimate of natural mortality and an initial estimate of hunting mortality. Because of the highly selective nature of the various hunts on harp seals, estimating these parameters is difficult (Lett and Benjaminsen 1977; Lett et al. 1979; Mohn 1979). Lett and Benjaminsen (1977) calculated the total mortality rate for two periods from changes in age frequencies within samples of molting males, assuming these to be representative of the population age structure. Natural mortality was then calculated by solving two simultaneous equations equating hunting mortality and natural mortality to total mortality. This required estimating the proportional change in the hunting mortality for the two periods, which they did by estimating the change in hunting effort, defined without justification, as number of men involved in the hunt multiplied by total horsepower of vessels used multiplied by number of days the hunt lasted divided by tonnage of vessels. Lett et al. (1979) regarded this method as "rather suspect." Winters (1978) also estimated total mortality using the age composition data of molting males. Hunting mortality was calculated using pup production estimates from the survival index method, and natural mortality obtained by subtraction from the total mortality, calculated from catch curves corrected for changes in recruitment. Lett et al. (1979) estimated natural mortality using pup production determined by the survival index method, information on maturity, sex ratio, fertility rate, and the age composition of seals in molting concentrations. In all of the above methods of estimating natural mortality, the number of steps involved in the calculation add greatly to the imprecision of the estimate. Winters (1978) estimated M to be 0.098 and Lett et al. (1979) gave an esti-

mate of 0.1. However, as the methods are very similar, both depending on the age composition of molting males and estimates from survival indices, this agreement cannot be taken as support for this value of M. For example, W. E. Ricker (DFO, Pacific Biological Station, Nanaimo, B.C., unpublished data), estimated M to be 0.08, whereas Beddington and Williams (1980) derived an estimate of 0.1375. Any of these values of average natural mortality for seals 1 yr and older are reasonable for the harp seal; indeed any value between 0.05 and 0.15 is well within the bounds of possibility. The difference in annual survival for these two values is only 9% (95−86%). However, this difference accumulates over time and after 10 yr the proportion still alive is 61% for $M = 0.05$ and 20% for $M = 0.15$. Thus, the difference between the two mortality schedules can be detected with a 10-yr time series of data.

Are Samples of Molting Seals Really Random?

The analyses of Winters (1978) and Lett et al. (1979) both use samples of molting harp seals to estimate natural mortality. Lett et al. (1979) also used them to initiate their cohort analysis. Beddington and Williams (1980) used the age distribution of molting males to estimate the 1952 population age distribution. Because they have been frequently used, it is important to ask: are the samples of molting male harp seals representative of the age distribution of the population?

Suppose in year t we obtain a random sample of animals whose frequencies within the sample are $f_1, f_2 \ldots f_i \ldots f_n$, where i is age and n the final age or age-group (e.g. 8+ animals). In year $t+1$ another random sample is taken and we calculate the frequencies $f_2, f_3 \ldots f_{i+1}, \ldots f_{n+1}$, the new incoming cohort being ignored. If the mortality rates are the same at each age, then f_i in year t will equal f_{i+1} in year $t+1$. The two age distributions can be compared using either a χ^2 or G test: a significant result indicates either that hunting mortalities are not equal or that the sample is not random. Variation in hunting mortalities will have to be very large to generate a shift in the distribution as it is necessary to shift the population age distribution. The hunting mortality on adult seals is far too small (Lett and Benjaminsen 1977; Winters 1978) to be capable of causing such a shift, and hence a significant G value indicates nonrandom sampling.

Reasonably large samples of molting males are available for the years 1968, 1969, 1970, 1971, 1973, 1974, and 1976. Numerous pairwise comparisons are available: we used the following procedure to select one particular set. To compare 1968 to other years we used the 2 to 9+ age distribution in 1968; thus this age distribution was compared to the 3 to 10+ in 1969, 4 to 11+ in 1970, and so forth. To compare 1969 to other years we used the 3 to 10+ age distribution in 1969; thus this age distribution was compared to the 4 to 11+ in 1970, the 5 to 12+ in 1971, and so forth. The same methodology was used when comparing years 1970−74 to other years. Each comparison has eight classes. There are a total of 21 possible comparisons; of these 7 were significantly heterogeneous indicating that the samples are not random. Correcting for the possible overrepresentation of 2-, 3- and 4- yr-olds in the sample using the correction factors derived by Sergeant (1976b) or Bowen and Winters (1979) did not remove the significant deviations. These tests are not independent as a subset of the data from one comparison is used in another comparison. However, the occurrence of significant deviations suggests caution in using the data. A detailed examination of the data indicates that the deviations are not caused by any systematic bias, but rather by particular age-groups being over- or under-represented in the sample. One was this could arise is if animals of the same age tended to herd together. In fact this appears to be the case. Sergeant (1965) and Øritsland (1971) report that in late March molting patches are composed of immatures of both sexes and adult males occur in separate patches. Later these age-groups mix to a greater extent. Adult females enter the molting patches more gradually and become fully represented only by late April.

The above analysis suggests that the samples of molting males may correspond to the age structure of the population, but that several years of data should be used to locate possible deviant age-classes or even whole samples that might by chance not be representative. Unless these sources of heterogeneity are taken into account, estimates of natural mortality that depend upon these data should be viewed with caution. Because of the low total mortality rate, small biases in the age distribution potentially may lead to large errors in estimation.

The problem is likely to be much less in using male molting samples to estimate an initial age distribution for a simulation model. In this case small deviations in individual frequencies will be of little consequence. Of importance is the possible occurrence of an overall skew in the distribution. This can be avoided by examining several years of data.

The Survival Index Method

In this section we give the mathematical rationale for this method and indicate sources of bias.

As defined by Winters (1978) the survival index is

$$(1) \qquad \mathrm{SI}_{a,t} = \frac{\text{total catch} \times C_{a,t}}{\sum_j C_{j,t} \sum_i C_{a,i}}$$

where $C_{a,t}$ is the catch of animals of age a at time t and the two denominators are the column and row totals, respectively, of the age matrix. SI is plotted against pup kill and an estimate of pup production obtained from the pup kill at which SI equals zero. It is clearly necessary in applying this method to assume that pup production does not change significantly over the period of time being considered. For this reason Winters (1978) used only blocks of 5 yr. What other assumptions are inherent in the method?

Confining our attention initially to a single age-group, we can show that $\mathrm{SI}_{a,t}$ is proportional to the frequency of that age-group in the population provided that the partial recruitment multiplier shows no systematic trend over time; i.e. on average the multiplier remains the same. This is the same assumption made by Beddington and Williams (1980) in their χ^2 method. This assumption may be reasonable, but it has never been rigorously tested. Because pup production is assumed constant, it is reasonable to assume a constant population size N. Hence

$$(2) \quad SI_{a,t} \propto f_{a,t} \propto \frac{[N_{o,t-a} - C_{o,t-a}]e^{-\sum_{i=1}^{t}(F_i + M)}}{N}$$

where $f_{a,t}$ is the frequency, $N_{o,t-a}$ pup production in year $t - a$, $C_{o,t-a}$ the pup kill in that year, and F_i and M the hunting and natural mortality rates from $i = 1$ to $i = t$. The last term will be approximately the same for cohorts of the same age and hence

$$(3) \quad SI_{a,t} \propto f_{a,t} \propto \frac{N_{o,t-a} - C_{o,t-a}}{N}$$

which verifies that there should be a linear relationship between the survival index and pup kill, at least when only a single age-group is considered. Nevertheless, the lack of independence between the survival indices of different cohorts makes the use of linear regression methods, strictly speaking, invalid. Thus the intercept may not be an unbiased estimate of pup production. Now suppose the population is changing with time; letting the population size be represented by the function $g(t)$ we have

$$(4) \quad SI_{a,t} \propto f_{a,t} = \frac{g(t - a)p - C_{o,t-a}}{g(t)}$$

where p is the proportion of the population pregnant. Because the population cannot change much from year to year, the ratio $g(t - a)/g(t)$ will be close to 1 permitting the approximation

$$(5) \quad SI_{a,t} \propto f_{a,t} \simeq p - \frac{C_{o,t-a}}{g(t)}.$$

From the above it can be seen that the estimate of pup production depends not only upon the change in population size, but also the direction of the change in the pup kill. If the population is decreasing and the kill increasing, the intercept on the x- (pup kill) axis will be reduced giving an underestimate of pup production, whereas if the kill is decreasing the intercept will be extended giving an overestimate. During the period 1950 to 1970 the pup kill fluctuated widely from 150 000 to 350 000 but did not show any trend. Thus although individual estimates may be over- or under-estimates due to these fluctuations, there should be no consistent bias. Because of the averaging over blocks of 5 yr, we would expect the estimate to lag behind the correct value, a phenomenon found in the simulation study of Beddington and Williams (1980).

To be able to combine survival indices for the same cohort over a number of years we require that they all estimate a common value. Now

$$(6) \quad SI_{a,t} = \frac{\text{total catch} \times f_{a,t}}{\sum_i f_{a,t} E_i N_i}$$

where E_i is the exploitation rate. We thus require that $f_{a,t}/\sum_i f_{a,t} E_i N_i$ and $f_{a+1,t+1}/\sum_i f_{a+1,t} E_i N_i$ estimate a common value, which in general, they do not.

Although a method may be biased in principle, in practice this bias may be of minor consequence. To assess this possibility requires a simulation study in which the survival index method is used to estimate pup productions from a simulated population that is a reasonable approximation to the real situation. Beddington and Williams (1980) used this approach to examine the reliability of the survival index in tracking a declining pup production. The error ranged from about 10 to 20%. Several attempts have recently been made to formalize the survival index method (K. I. Ugland, Department of Marine Zoology, University of Oslo, P.O. Box 1064, Blindern, Oslo 3, Norway, unpublished data; J. G. Cooke, International Institute for Environment and Development, London, England, unpublished data). The results of these analyses also suggest that the survival index method as previously used may not be seriously in error. However, until these studies are completed, the results from the survival index method should be viewed with caution.

The χ^2 Method

The χ^2 method used by Beddington and Williams (1980) consists of comparing the age structure of the population predicted from a simulation model with that obtained from either the large vessel or landsmen's hunt. As both of these hunts are age selective it is necessary to incorporate these as parameters to be estimated by their method. By this method they estimate an average 1+ mortality rate (M) of 0.1375 and predict a decline in the population under the present quota. Mortality in the 1st year (M_0) was predicted to decline from 0.45 in 1952, the 1st year of the simulation to a plateau of 0.12 from 1971 onwards. Are these estimates of natural mortality reasonable?

It is a consensus among published analyses of harp seal population dynamics that by 1952 the population was depleted. Thus we may assume (a) that at some time in the past the population was larger, and (b) that if hunting mortality were removed the population would probably increase in size.

Any model that attempts to simulate harp seal population dynamics should show an increase in population size after 1952 if hunting mortality is set to zero. It is possible that environmental conditions have changed such that the population would decline in the absence of hunting, but this seems unlikely and one should view models that predict such a decline with considerable caution. A population in a stable age distribution in which the life table components are set at the 1952 level should increase in the absence of hunting. In a stable age distribution we have

$$(7) \quad \sum_{a=1}^{\infty} e^{-M_0} e^{-M(a-1)} P_a = 1$$

where M_0 is the mortality rate in the 1st year, M the mortality rate in subsequent years, and P_a the age-specific pregnancy rate. Using the pregnancy formula for the early 1950s of Beddington and Williams (1980), and assuming a 1:1 sex ratio, we have

$$(8) \quad \sum_{a=6}^{a=8} 0.5e^{-M_0 - M(a-1)} P_a + \sum_{a=9}^{a=\infty} 0.5e^{-M_0 - M(a-1)} P_{\max} = 1$$

where $P_{\max}$ is the maximum proportion pregnant, achieved by age 9. Substituting in the appropriate values and rearranging,

$$(9)\quad 0.5\,(0.23e^{-5M} + 0.59e^{-6M} + 0.80e^{-7M}) + \frac{0.85e^{-8M}}{2(1 - e^{-M})} = e^{M_0}.$$

If the mortality in the 1st year of life equals that in subsequent years, from eq. 9 then $M_0 = M = 0.155$. Beddington and Williams (1980) estimated $M_0 = 0.45$ and $M = 0.1375$; substitution of $M_0 = 0.45$ in equation (9) yields a maximum value for M of 0.131. Thus the maximum value of M theoretically possible is less than that estimated by Beddington and Williams.

The natural mortality of the 0-group animals (M_0) is predicted to have declined after 1952 and hence at some point after 1952 the population would have been able to increase in the absence of hunting. However, the fact that the χ^2 method predicts parameter values at the start of the simulation that are less than required for an unharvested population suggests that there is something amiss with the method. Recent analyses (N. O. Jacobsen, Institute of Marine Research, P.O. Box 5011 Berger-Nordnes, Norway, unpublished data; W. K. de la Mare, International Institute for Environment and Development, 10 Percy St., London W1P 0DR, England, unpublished data) indicate that estimates of pup production and natural mortality are confounded. For this reason, it was concluded at a recent meeting of the ICES Ad Hoc Working Group on Harp and Hooded Seals "that previously reported estimates of M by such methods should not be considered" (Anon. 1982).

An Alternative Method

The method we have used is similar to that of Beddington and Williams in that it consists of comparing the output of a simulation model with a set of independent observations. In the present analysis those observations are estimates of pup production in 1967, 1971, 1978, 1979, and 1980. We have adopted a maximum likelihood type of approach to estimate the joint probability of the pup production at the initiation of the simulation and the average natural mortality rate of 1+ seals.

Consider two trajectories of pup production from a harp seal simulation model. Suppose in 1978 one trajectory passes through N, the estimate of pup production from the mark–recapture analysis, and the other through $N + 3$ SE, where SE is the standard error of the estimate. Because the second trajectory lies outside the 95% confidence region of the mark–recapture estimate, we would conclude that the set of parameter values that produced this particular trajectory is highly unlikely. On the other hand, the set of parameter values that produces a trajectory that passes through N can be considered a "likely" set. Consider now any two trajectories from the simulation model. Let the predicted pup productions from 1978, 1979, and 1980 be $N_1(78)$, $N_1(79)$, $N_1(80)$, and $N_2(78)$, $N_2(79)$, $N_2(80)$ for the two trajectories. Which trajectory is the more probable? Suppose we knew that the pup productions were distributed normally as $N(\mu_{78}, \sigma_{78})$, $N(\mu_{79}, \sigma_{79},)$ and $N(\mu_{80}, \sigma_{80})$ for the years 1978, 1979, and 1980. In this case the probability that the pup productions in 1978, 1979, and 1980 were $N_1(78)$, $N_1(79)$, and $N_1(80)$ would be the product of the probabilities.

$$(10)\quad P = \phi\left(\frac{N_1(78) - \mu_{78}}{\sigma_{78}}\right)\phi\left(\frac{N_1(79) - \mu_{79}}{\sigma_{79}}\right) \times \phi\left(\frac{N_1(80) - \mu_{80}}{\sigma_{80}}\right)$$

where $\phi(x)$ is the probability of a value x given a normal distribution $N(0, 1)$.

Similarly the probability that they were $N_2(78)$, $N_2(79)$, and $N_2(80)$ would be

$$(11)\quad P = \phi\left(\frac{N_2(78) - \mu_{78}}{\sigma_{78}}\right)\phi\left(\frac{N_2(79) - \mu_{79}}{\sigma_{79}}\right) \times \phi\left(\frac{N_2(80) - \mu_{80}}{\sigma_{80}}\right).$$

The "more likely" parameter set is that which gives the largest P. By calculating P for all parameter sets we could arrive at a "most likely" set. Although estimation of this set is important, it is as important to estimate the confidence region about this combination. In the present case we are estimating two parameters and hence the probability distribution can be represented as contours on an x–y plane, the two axes being natural mortality and pup production at the start of the simulation. To estimate the 95% confidence region about the "most likely" combination, we integrate over the surface and find the set of combinations that comprises 95% of the total integral. Although one might choose to locate this region by a variety of criteria, a logical choice is to assume that the boundary of the confidence region has the same value of P (i.e. we take horizontal "slices" through the distribution until we arrive at the contour that encloses the specified volume).

We do not know the actual probability distributions of pup productions, but we may use as estimates of these the values derived from the mark–recapture analyses (Bowen and Sergeant 1983). Estimates of harp seal pup production in the northwest Atlantic from mark–recapture studies are as follows: 1978, 505 704 ± 77 337 ($\bar{x}$ ± 1SE); 1979, 489 397 ± 70 794; and 1980, 449 952 ± 80 586 (Bowen and Sergeant 1983).

The 1978, 1979, and 1980 mark–recapture estimates "anchor" the trajectories in the late 1970s but we also require an "anchor point" for the beginning of the simulation to constrain the parameter set reasonably. There are no mark–recapture estimates for this earlier period. However, the marked variation in pup kills of some adjacent years can be used to derive an appropriate statistic. This statistic can also be used to estimate pup production directly and is derived as follows: Let $n_{a,t}$ be a sample of seals of age a taken at time t. Then $n_{a,t}/(n_{a,t} + n_{a-1,t})$ is the proportion of cohort a relative to its adjacent cohort, $a - 1$. By the central limit theorem this proportion, say Q, can be assumed to be normally distributed with mean Q and variance $Q(1 - Q)/(n_{a,t} + n_{a-1,t})$.

Estimates of Q can be obtained from the samples of molting males. These estimates can be used to assign probabilities to the values of Q predicted by the simulation model. The probability of observing any particular trajectory is the product of these probabilities and those obtained using the mark–recapture estimates.

To estimate Q we selected only those pairs of cohorts in

which the kill of one was very different from the other. In the absence of hunting or when the kill history of adjacent cohorts is very similar, Q will be close to 0.5. Under these circumstances, Q will have little power to discriminate between different combinations of natural mortality and initial pup production. This can be seen from the following approximate formula for estimating pup production using $n_{a,t}$ and $n_{a-1,t}$. Let $N_{o,t}$ be the pup production in year t and $C_{o,t}$ the kill of whitecoats and beaters. As most of these animals are killed over a short period of time, we have, approximately

$$(12)\quad \frac{(N_{o,t} - C_{o,t})e^{-M}}{(N_{o,t} - C_{o,t})e^{-M} + N_{o,t+1} - C_{o,t+1}} \simeq Q.$$

The breeding portion of the population consists of many age-classes. Thus, there will be little change in the population size between years and hence $N_{o,t} \simeq N_{o,t+1}$. Rearranging equation (12) we have

$$(13)\quad N_{o,t} \simeq \frac{e^{-M}C_{o,t}(1 - Q) - QC_{o,t+1}}{e^{-M} - Q(1 + e^{-M})}.$$

As $C_{o,t}$ approaches $C_{o,t+1}$, Q approaches 0.5 and the denominator approaches $0.5(e^{-M} - 1)$. Equation (13) then becomes very sensitive to sampling fluctuations, the confidence limits increasing rapidly. That confidence limits be small enough to be of any use, $C_{o,t}$ and $C_{o,t+1}$ must be quite different. Thus for the simulation model to be able to discriminate between combinations of parameters, we require estimates of Q that are markedly different from 0.5. There are a number of years in which the pup kills are sufficiently different that Q is reasonably different from 0.5: of these we selected the pairs of years 1967/1968 and 1971/1972. Earlier pairs were discarded because we chose to initiate the simulation model in 1967. The reasons for this choice are:

1) Øritsland (1971) and Benjaminsen and Øritsland (1975) noted that the pup kill in 1967 was extremely large and by adding to this all those seals from this cohort caught since then we can place an absolute minimum bound for pup production in 1967. Up to 1980 a total of 295 658 of the 1967 cohort had been taken.

2) Few reliable data on age-specific pregnancy rates are available before 1964. This is a component of the simulation model and as there has been a shift in these rates an earlier start to the model would necessitate adding the earlier pattern of pregnancy as a variable to be estimated: the possible increased uncertainty due to the extra parameters would unlikely be offset by the increased time span available.

3) By 1967 it is generally assumed that the population was substantially reduced from its pristine levels. It therefore seemed unlikely that density-dependent changes in mortality rates have occurred since then and thus we could reasonably assume a constant rate. The analyses of both Winters (1978) and Beddington and Williams (1980) suggest that at least since the early 1970s pup mortality, M_0, has equalled adult mortality, M. We have examined both the case in which $M_0 = M$ and the case in which M_0 is greater than M. In all cases M_0 and M are assumed to be constant over time.

Because of potential errors in age determination (Doubleday and Bowen 1980), we used only ages less than 11 yr to estimate Q. For the 1967/68 cohorts five samples of molting males are available (1970, 1971, 1973, 1974, 1976). The samples are homogeneous (Table 1) and show no trend. Three years are available for the 1971/72 combination (1974, 1976, 1979); these samples are homogeneous and no trend is detectable (Table 2). Because the samples are homogeneous they can be pooled, yielding estimates of Q of 0.2691 (n = 301) and 0.3803 (n = 213) for 1967/68 and 1971/72, respectively. The estimated standard deviations are 0.0256 and 0.0333, respectively.

TABLE 1. Testing for bias in the estimation of Q for the 1967 and 1968 cohorts.[a]

	1967 cohort		1968 cohort	
Year	Age	No.	No.	Age
1970	3	11	25	2
1971	4	15	26	3
1973	6	31	89	5
1974	7	16	70	6
1976	9	8	10	8
		81	220	

[a]G = 7.938, df = 4, P = 0.09, Q = 81/301 = 0.2691.

TABLE 2. Testing for bias in the estimation of Q for the 1971 and 1972 cohorts.[a]

	1971 cohort		1972 cohort	
Year	Age	No.	No.	Age
1974	3	57	105	2
1976	5	9	15	4
1979	8	15	22	7
		81	132	

[a]G = 0.386, df = 2, P = 0.18, Q = 81/213 = 0.3803.

DESCRIPTION OF THE SIMULATION MODEL

The year is divided into four periods with pup production occurring as a "point event" at the interface of two of these periods. This division is based on the type of hunting occurring during different times of the year. Immediately following pup production the 1+ seals are subjected to 3 mo of hunting from large vessels and longliners, the former being the large sealing ships that remain at sea for several months and the latter the smaller land-based boats. During this period the adults are slowly migrating northwards and the next component of the model comprises the Greenland and Canadian Arctic hunts which take place over 4 mo during the summer. Thereafter there is a period of 2 mo in which the seals are not hunted. At the end of this period a new calendar year begins and the age vector is updated. In the final period of 3 mo, the seals migrate southwards to their feeding and whelping areas and are harvested by shooting and netting. The hunting schedule on the young-of-the-year (whitecoats and beaters) differs slightly from that on the adults in that pups are taken for 1 mo

TABLE 3. Percentage of females pregnant by age and year.

Age	Year							
	1965	1966	1967	1968	1969	1970	1978	1979
2	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	6.1
4	3.3	0	0	0	4	0	2.5	23.8
5	11.4	11.1	21.1	31.6	16.0	23.1	60.5	53.3
6	54.1	35.3	60.6	70.0	43.8	50.0	90.0[a]	100.0[a]
7+	83.7	85.0	90.1	88.1	88.0	86.3	82.0	93.3

[a]Combining with 7+ 1978, 6+ = 84.3%, 1979, 6+ = 94.3%.

by the large vessels, and beaters are hunted for 2 mo by landsmen. The number of seals of age a remaining after hunting period j in year t, $N_{a,j,t}$, is given by the equation

$$(14) \quad N_{a,j,t} = N_{a,j-1,t}e^{-(F_{a,j,t}+MT)}$$

where $F_{a,j,t}$ is the hunting mortality rate during the period j, M is the instantaneous natural mortality rate, and T is the proportion of the year over which hunt j takes place. $F_{a,j,t}$ can be estimated by iteration from the relationship

$$(15) \quad C_{a,j,t} = \frac{N_{a,j-1,t}F_{a,j,t}(1 - e^{-(F_{a,j,t}+MT)})}{F_{a,j,t} + MT}$$

where $C_{a,j,t}$ is the catch of seals of age a and hunt j in year t. Solving for $F_{a,j,t}$ used considerable computer time relative to the remainder of the simulation. For this reason we used the approximation given by Pope (1972),

$$(16) \quad N_{a,j,t} = (N_{a,j-1,t} - C_{a,j,t}e^{MT/2})/e^{MT}.$$

This approximation is reasonable provided $M < 0.3$ and $F < 1.2$: both of these constraints apply to the present model. For reassurance we made runs differing only in the method of estimating $N_{a,j,t}$: the differences in population size after running the model to 1979 were inconsequential.

At least during the last 10 yr the age at maturity in seals has declined (Bowen et al. 1981). For the model we require the relationship between age and pregnancy rate. Data on this are presented in Table 3. Reproductive samples were collected in late term to avoid errors due to early pregnancy failure. Excepting the 1979 data, there appears to have been no change in the pregnancy rate of seals aged 2, 3, or 4. More data are required to substantiate the apparent increase in the proportion of seals pregnant at age 4 and perhaps age 3 in 1979. In the present analysis we have assumed a constant rate for these age-classes. At age 7 the maximum pregnancy rate is achieved and seals age 7 and older have been combined. The percentage pregnant at ages 5 and 6 show a significant increase over time (for age 5: arcsine $\sqrt{\%\ \text{Preg}\ 5} = 18.22 + 2.085$ yr, $r = 0.936$, $P < 0.01$, and for age 6, arcsine $\sqrt{\%\ \text{Preg}\ 6} = 39.50 + 2.091$ yr, $r = 0.845$, $P < 0.01$). In 1978 and 1979 the maximum pregnancy rate is achieved at age 6 and for the purposes of regression analysis the 6+ groups were used for these 2 yr. As is usual with percentages the dependent variable, percentage pregnant, was transformed using the arcsine square root transformation. The proportions pregnant by age and year used in the model were obtained as follows. The proportion pregnant at age 4 was obtained by pooling across years; the same procedure was used for the 7+ animals except that animals aged 6 in 1978 and 1979 were also included. Thus at age 4, 4.6% of females were pregnant and at age 7+ (6+ in 1978, 1979) 87% of females were pregnant. The percentage pregnant at ages 5 and 6 were calculated using the appropriate regression equations.

TABLE 4. Comparison of samples of male molting harp seals used to estimate the production of 7+ in 1967.[a]

Year	Age-groups	No.	Age-groups	No.
1969	3−8	166	9+	299
1970	4−9	45	10+	59
1971	5−10	59	11+	96
1973	7−12	122	13+	46
1974	8−13	130	14+	149
1976	9−14	39	15+	68

[a]$\chi^2 = 74.4$, df = 5, $P < 0.001$.

The final component of the model is the initial age distribution. As discussed earlier, in general, the samples of molting male harp seals appear to be a reasonable representation of the population age structure. An analysis of the sensitivity of the simulation model indicated that the most important component of the age structure is the ratio of fully mature seals (7+) to immature (ages 1−6). To estimate the 1967 age structure we therefore proceeded in two stages. First we estimated the proportion of 7+ in the 1967 1+ population from their representation in molting samples from 1969, 1970, 1971, 1973, 1974, and 1976 (Table 4). The later samples comprise age-groups in which aging errors may be significant. However, because we consider groupings of at least 6 yr, the effect is likely to be small. There is significant heterogeneity between samples ($\chi^2 = 74.4$, df = 5, $P < 0.001$) indicating that at least one sample is biased. Almost the total contribution to the χ^2 statistic comes from the 1973 sample; elimination of this year reduces the χ^2 value to 9.85. This value is slightly greater than the 5% level, the critical value being 9.49, and is due primarily to the 1974 sample (Table 5). However, the total effect on the percentage of 7+ is small: using all years the percentage is 60.5%, whereas eliminating 1974 changes the value to 62.8%. The percentage of 7+ across the individual samples range from 64% in 1969 and 1976 to 53% in 1974. From runs of the

TABLE 5. Comparison of samples of male molting harp seals used to estimate the proportion of 7+ in 1967. The sample from 1973 has been eliminated.

Year	Ages 1–6 in 1967	χ^{2a}	Ages 7+ in 1967	χ^2	%7+
1969	166	1.74	299	1.14	64
1970	45	0.36	59	0.24	57
1971	59	0.09	96	0.06	62
1974	130	3.50	149	2.29	53
1976	39	0.26	68	0.17	64

[a]Individual χ^2 values.

simulation model with different percentages of 7+ seals in 1967, we found that the predicted replacement yield increased as the percentage of 7+ in the 1967 age distribution was increased. We therefore adopted a conservative approach and set the 1967 percentage of 7+ seals at 55%.

The second stage of the estimation of the 1967 age structure consisted of estimating the individual frequencies of ages 1–6. We took as an initial estimate of the age structure the relevant ages from the molting samples in 1969, 1970, and 1971. A population size for 1967 was then estimated by setting the 1967 pup production and calculating the size of each cohort using the age distribution and age-specific pregnancy rates. We then projected backwards using cohort analysis to obtain estimates of pup productions for the years 1961 to 1966 and adjusted the frequency of the 1–6 age-classes to obtain a set of pup productions that were reasonably consistent. Consistency was defined as a set of productions that showed no major shifts between adjacent years. Adjustment was required only for age-groups 1 and 2 (for age 1 from 6.4 to 8.0% and for age 2 from 4.7 to 11.0%). As we were concerned only with trends, the pup production and natural mortality rate used to initiate the cohort analysis were not critical. The frequencies of ages 1 through 6 used in the model were 8.0, 11.0, 5.3, 5.5, 7.0, and 8.2%, respectively.

Analysis

Previous analyses have been based on the age structure of total annual harp seal catches given by Lett and Benjaminsen (1977). The present analysis uses revised catch-at-age data given in Bowen (1982). These data differ from those of Lett and Benjaminsen in that they include animals 26 yr of age and older and catches from the Canadian Arctic and West Greenland. They also correct a bias in the age composition of inshore catches which led to overestimation of the kill of mature seals, particularly in recent years.

A priori it may seem reasonable to assume that the natural mortality rate decreases, at least initially, with age. However, there are several reasons for suspecting that this may not be the case for harp seals. Firstly, the environment into which the pups are born is relatively free of predators and secondly, conditions on the ice are relatively aseptic making death from infection unlikely. Probably the greatest source of mortality during the whitecoat stage is premature break up of the ice or ice-rafting which may kill some pups (Sergeant 1976a). Such a phenomenon does not, however, appear to be a common occurrence (D. E. Sergeant, Arctic Biological Station, Ste. Anne de Bellevue, Que., personal communication). The growth rate in the 1st year of life is very high, the animal attaining ≈70% of its adult body length by age 1 and ~50% of its maximum weight (Sergeant 1973). If there is any change in mortality with age, the major portion is likely to occur in the 1st year when seals are presumably inexperienced at foraging and are growing at a substantial rate. In the absence of any data on the age-specific mortality rate, we have examined two possibilities. Firstly, we have assumed that $M_0 = M$ and secondly, that $M_0 = 3M$, i.e. that mortality in the 1st year of life is 3 times that of 1+ animals (see Discussion for a com-

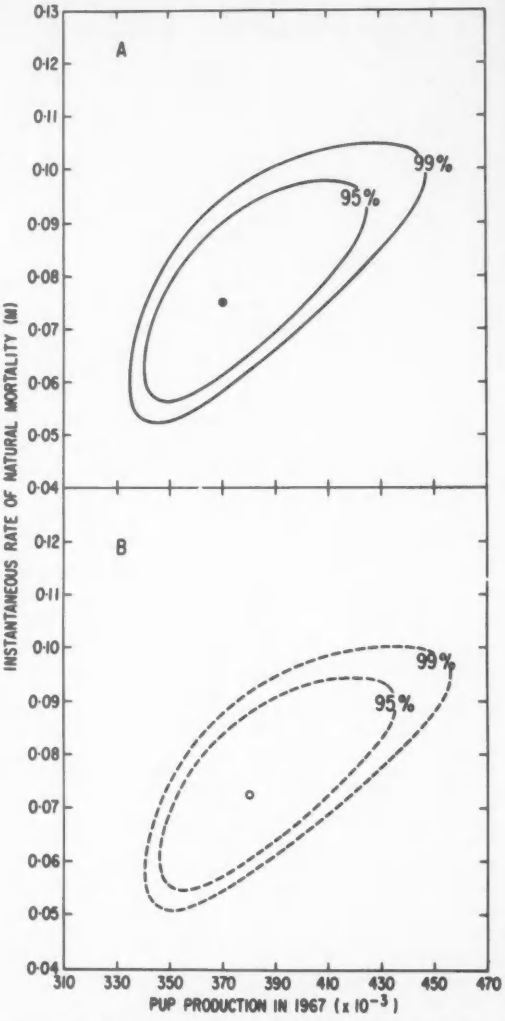

FIG. 1. Confidence regions for the 1967 pup production (thousands) and natural mortality, M, for the two mortality schedules. A: $M_0 = M$, B: $M_0 = 3M$.

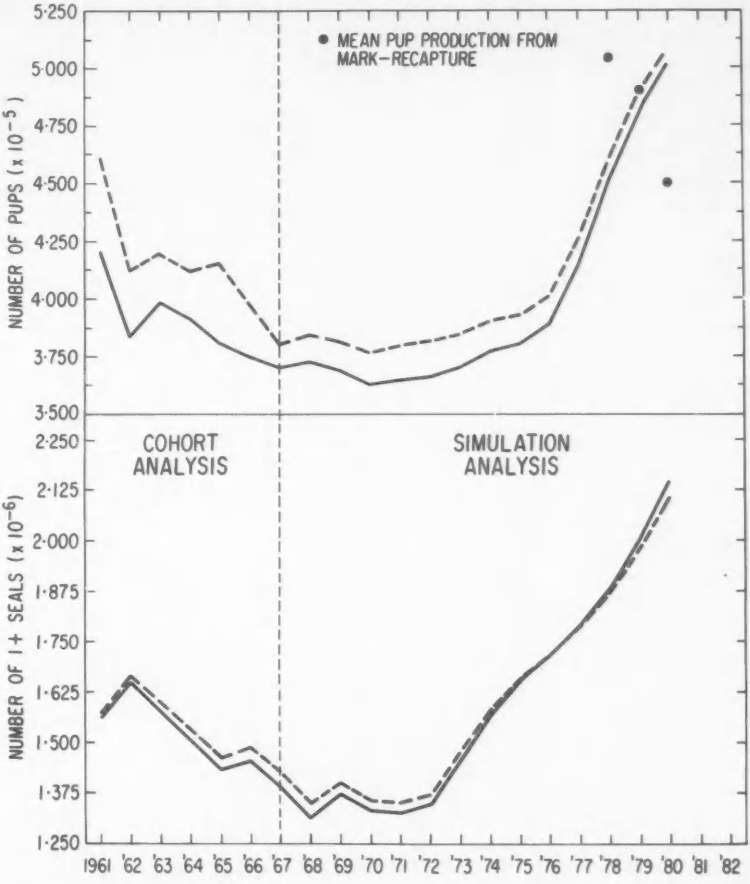

FIG. 2. Estimates of 1+ population sizes (millions) and pup production (hundred thousands) from 1961 to 1980 using the 'most likely' estimates of M and 1967 pup production. (—) $M_0 = M$, (···) $M_0 = 3M$.

parison of mortality rates in pinnipeds).

Using the model outlined above we estimated the probability associated with combinations of M and 1967 pup production. For computational convenience this probability was multiplied by a constant, thereby making the largest value approximately 12. A value of e^{-20} was used to delimit the range in the combinations of M, and pup production examined. Confidence regions were estimated in the manner described: because the 95% confidence region may be underestimated the 99% region was also estimated. The results for the two mortality schedules are shown in Fig. 1.

For $M_0 = M$, the "most likely" combination is $M = 0.075$ and $N_{67} = 370\,000$: for $M_0 = 3M$, the "most likely" combination is $M = 0.0725$ and $N_{67} = 380\,000$. The population and pup production from 1961 to 1981 are shown in Fig. 2 for these two combinations. There is an initial increase in pup production in 1972: this is due to the recruitment to the breeding population of the 1965 year-class, which was large because of a relatively low pup kill (188 183; Bowen 1982). The results of the decrease in the level of kill starting in 1972 become evident in 1977 when the pups from 1972 recruit into the breeding population. Prior to 1977 there is a slow increase in pup production resulting from the decreased kill of 1+ seals.

Isopleths of predicted pup production and 1+ population size in 1982 are shown in Fig. 3 and 4. The 99% confidence limits of pup production in 1982 are ~350 000 and 780 000, with associated 1+ population sizes of 1.4×10^6 and 3.5×10^6.

To calculate the replacement yield, defined on the 1+ population, we used the following approximate method.

$$(17)\quad N_{1+,t+1} = (N_{1+,t} - qCe^{-M/2})e^{-M} + [N_{0,t} - (1-q)C]e^{-M_0}$$

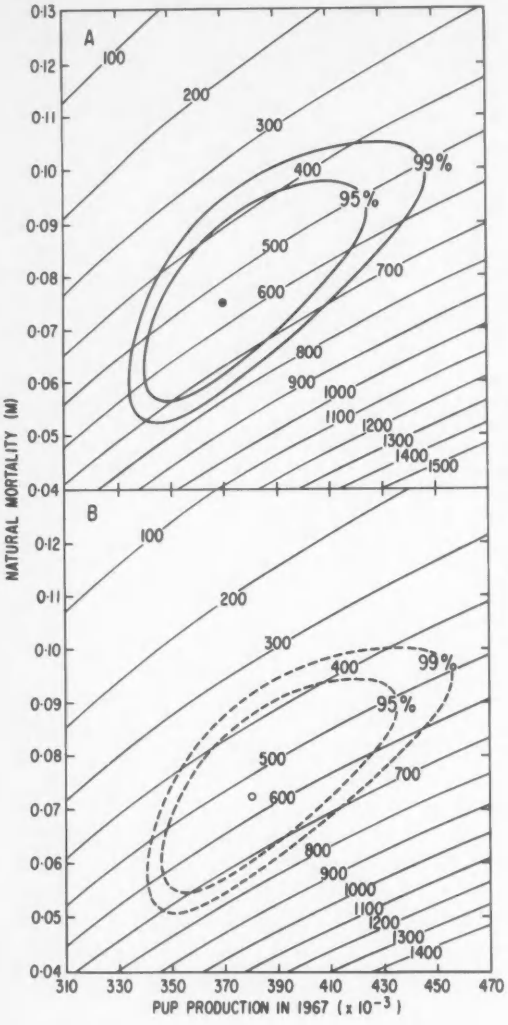

FIG. 3. Isopleths of pup production (thousands) in 1982 for different combinations of M and 1967 pup production (thousands). The 95 and 99% confidence regions are superimposed. A: $M_0 = M$, B: $M_0 = 3M$.

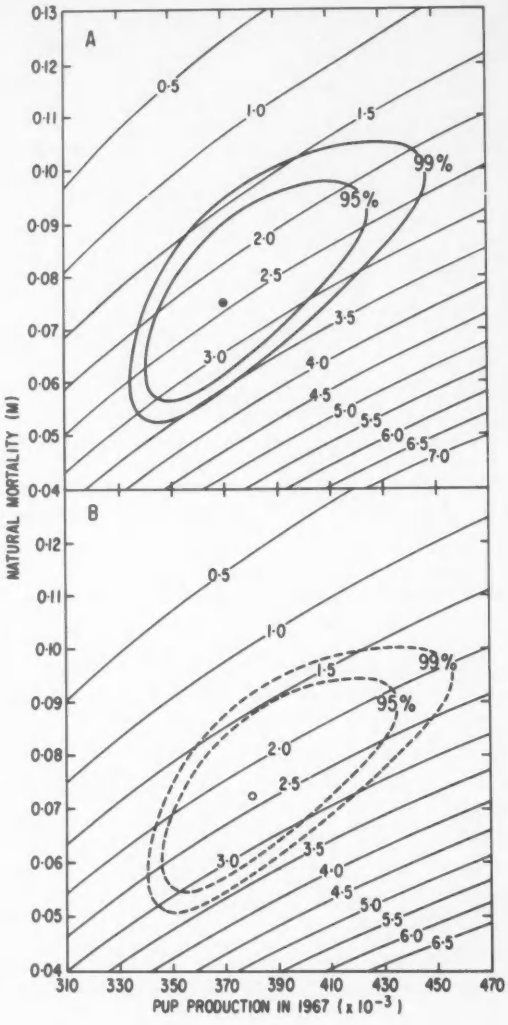

FIG. 4. Isopleths of 1+ population size (millions) in 1982 for different combinations of M and 1967 pup production (thousands). Confidence regions as in Fig. 3. A: $M_0 = M$, B: $M_0 = 3M$.

where $N_{1+,t}$ is the number of 1+ seals at time t
$N_{0,t}$ is the number of pups at time t
C is the replacement catch
q is the proportion of the catch that is allocated to 1+ seals. At present $q = 0.2$.

We require that $N_{1+,t+1} = N_{1+,t} = N$, (the last for notational convenience). Substituting and rearranging we have

$$(18)\quad C = \frac{N(e^{-M} - 1) + N_{0,t}e^{-M_0}}{e^{-M/2}q + e^{-M_0}(1 - q)}.$$

Tests of this equation over a range of parameter values indicated that it was satisfactory, the population either remaining stationary or increasing by less than 10% by 1991. The predicted replacement yields for 1982 are shown in Fig. 5. When $M_0 = M$ the replacement isopleth of 200 000

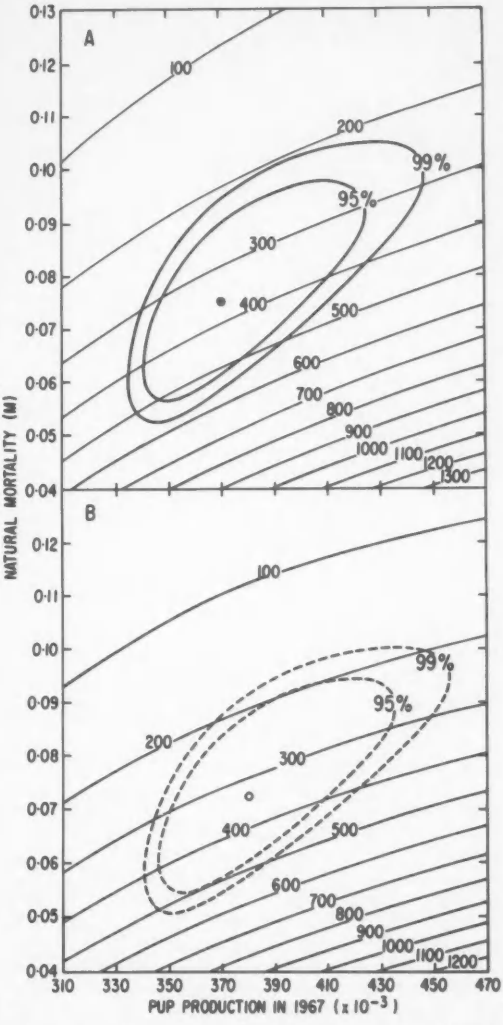

FIG. 5. Isopleths of replacement yield (thousands) in 1982 for different combinations of M and 1967 pup production (thousands). Ninety-five and 99% confidence regions are superimposed. A: $M_0 = M$, B: $M_0 = 3M$.

seals killed lies beyond the 99% boundary and when $M_0 = 3M$ the replacement isopleth lies on the 95% upper boundary. Thus there is a negligible probability that the present catch of ≈200 000 will cause the population to decline. Thus if the present quota is maintained the population should continue to increase. The predictions from Fig. 5 suggest that the present harvest may be well below the replacement yield.

The predicted increase in population size clearly depends upon the estimates of the mark–recapture experiments. Until data are available to substantiate these estimates further, we consider it unwise to attempt any precise evaluation of long-term yields.

Discussion

The rate of natural mortality is usually the most difficult parameter to estimate for an animal population. In the case of the harp seal it is difficult to obtain representative age-frequency samples, and these are often confounded by changes in recruitment and hunting mortality. Sergeant and Fisher (1960) estimated that the total annual mortality rate for immatures (ages 1–5) was higher than that for adults (ages 6–10), but they were unable to obtain a reliable estimate of 1st-year mortality. Recent authors have suggested that the data are not sufficient to discriminate between the mortality rates of immatures and adults. Generally the average M calculated for adults is assumed to hold for animals of all ages (Allen 1975; Benjaminsen and Øritsland 1975; Lett and Benjaminsen 1977; Winters 1978) or it is assumed that harp seals suffer somewhat higher rates during their 1st year of life as some function of population size (Lett et al. 1979; Beddington and Williams 1980).

Natural mortality rates in many mammals vary markedly from one age-class to another and often males suffer greater rates than females (Trivers 1972; Ralls et al. 1980). Caughley (1966) concluded that the typical mammalian mortality pattern is "U-shape" consisting of a juvenile phase characterized by initially low but steadily increasing rates of death. However, complete, accurate life tables for both sexes exist for very few species of mammals (Caughley 1966; Ralls et al. 1980).

Complete or partial life tables have been proposed for a number of species of pinnipeds: grey seals, *Halichoerus grypus* (Hewer 1964; Mansfield and Beck 1977); ringed seals, *Pusa hispida* (Smith 1975); harbour seals, *Phoca vitulina* (Bigg 1969); southern elephant seals, *Mirounga leaonina* (Laws 1960); and northern fur seals, *Callorhinus ursinus* (Smith and Polacheck 1981). Life tables for the ringed seal, harbour seal, and northern fur seal can be considered most reliable and in each case the mortality rate of immatures is higher than that of young adults. Ralls et al. (1980) found a similar pattern of age-dependent mortality in a number of nonmarine species. Thus the assumption of a constant M in harp seals 1-yr-old and older is unlikely. However, as yet it has not been possible to estimate reliably age-specific mortality rates for harp seals.

The question of whether 1st-year mortality in harp seals is higher than the average rate experienced by older animals is difficult to answer. Winters (1978) estimated the 1st year M of harp seals to be 0.10, although the validity of this estimate has been questioned. Lett et al. (1979) and Beddington and Williams (1980) found no evidence of higher M in the 1st year of life during the 1970s; however, both studies suggested higher rates may have occurred in the 1950s. Bigg (1969) estimated that 1st-year mortality and average adult mortality in harbour seals were equal, about 0.22.

In most pinnipeds 1st-year mortality is higher than that experienced by older seals and values of 30–60% are not

TABLE 6. Natural mortality estimates of pinnipeds from birth to weaning.

Species	Natural mortality at weaning (%)	Source
Harp seal	<1.0	Sergeant (unpublished data)
	0.93–3.3	Popov (1971)
Weddell seal	4.7–5.1	Stirling (1971)
Grey seal	14.1–35.0	Anderson et al. (1979)
	13.9–27.3	Bonner and Hickling (1971)
Northern fur seal	10.0 ($\bar{x}$)	Lander (1979)
	5.0–20.0	Ichihara (1974)
Southern fur seal		
Arctocephalus forsteri	15.0–26.0[a]	Mattlin (1978)
Southern elephant seal	0.8–6.8	Laws (1953)
	2.0–12.0	Carrick et al. (1962)
Northern elephant seal	15.8	LeBoeuf and Briggs (1977)

[a]Birth to 50 d.

uncommon (Smith 1975; Payne 1977; Reijnders 1978; Boulva and McLaren 1979; Lander 1979). Much of this mortality occurs before weaning, usually the result of starvation and/or trauma and varies from 10 to 35% with the exception of the harp seal, Weddell seal, and possibly the southern elephant seal (Table 6). In harp seals mortality from birth to weaning varies from about 1.0% or less for the northwest Atlantic population to only 3.3% for the White Sea population. Although we cannot dismiss the possibility of high post-weaning mortality, harp seals appear to differ from land-breeding pinnipeds in having a low preweaning mortality rate. Nevertheless, it seems only prudent to consider higher rates of 1st-year mortality than have been assumed in the past and given what we know about other species, $M_0 = 3M$ seems reasonable.

It is generally assumed that male and female harp seals suffer the same natural mortality rates. Lett et al. (1979) stated that this assumption is based on the observation that males and females have similar growth rates and achieve equivalent maximum ages (Sergeant 1973). For seven species of pinnipeds reviewed by Ralls et al. (1980), estimated mortality rates of adult males were higher than those of adult females, even in those species like the harp seal, where males and females are similar in size (i.e. harbour and ringed seal) or where females are actually larger than males (Weddell seal). Hence, it is likely that male harp seals experience greater mortality rates than do females. Nevertheless, based on data for ringed seals (Smith 1975) and harbour seals (Bigg 1969), these differences are probably small over much of the life span and are unlikely to bias our results significantly.

Our estimated pup productions to 1970 are in reasonable agreement with the estimates of Winters (1978). We estimate a lower natural mortality rate. Such a rate is necessary to permit the population to increase to the sizes estimated for 1978, 1979, and 1980. All methods of analysis (Winters 1978; Beddington and Williams 1980; and modified survival index methods presented at ICES, Anon. 1982) indicate a 1967 pup production of ~370 000. The reason for this results from the dependence of all methods on the contrast in pup survival: the contrast between 1967 and adjacent years is substantial and probably "drives" all the methods. The pup production estimated from the approximate formula (equation 13) is 359 000 which is very close to that obtained from the simulation approach. This estimate is insensitive to M, pup production being 362 000 for $M = 0.1$ and 368 000 for $M = 0.14$. Estimates of the 95% confidence bounds can be made by substituting $Q \pm 2$ SE. This gives values of 332 000–404 000 when $M = 0.075$ and 333 000–410 000 when $M = 0.1$. The lower 95% confidence bounds for the mark–recapture experiments are 354 000 for 1978, 351 000 for 1979, and 292 000 for 1980. The probability that pup production in these years was less than 410 000 (the upper confidence limit of the estimate of 1967 production) is 0.11, 0.13, and 0.31 for 1978, 1979, and 1980, repectively. Thus it is unlikely that the pup production in the late 1970s was less than that in 1967.

There is little difference in the results obtained for the two mortality schedules. This can be attributed to the low adult mortality rate: even a threefold increase in this rate during the 1st year of life has a minor influence compared to the kill. Although no precise point estimate of replacement yield can be made, the results indicate that the replacement yield is most likely substantially larger than the present quota.

Any simulation model, indeed any analysis, necessarily involves simplifications. We have assumed the natural mortality and pregnancy rates to be deterministic, the former remaining constant, the latter changing linearly with time. These assumptions are undoubtedly not strictly correct but it is unlikely that the variance in these components will be large. If there is any point in the life of the harp seal when mortality might be variable, it is in the 1st year of life. However, the fact that the survival index method appears to work reasonably well argues against extreme variability. Our greatest source of uncertainty is the relationship between the mortality rate and age. But, because the model is tuned to external observations, short-term projections of population trends should be reasonably close to reality. Nevertheless, the harp seal population, like all natural systems, must be managed cautiously with due cognizance of the uncertainty within both the analyses and the natural world.

Even after taking into account the uncertainties described above, the evidence is strong that the harp seal population is large and increasing. It thus provides an excellent opportunity to gain more insight into the biological parameters of the seal

population by adaptive management. The most obvious strategy is to vary the quota. A major problem of the present hunt is that because the quota is kept more or less constant over time, the relative changes in cohort size that permit the use of such methods as the survival index method are not evident. This is unfortunate as an analysis of the relative sizes of cohorts can be an important source of biological information. From this point of view it would be better to vary the quota, having it high in 1 yr and low in the next. Such a tactic would not endanger the seal population as it is large and is comprised of many age-groups, but it may not be economically or socially acceptable.

Our knowledge of the life history parameters and population dynamics of the harp seal is still inadequate to be anything but cautious in deciding upon management schemes. Management policies must take into consideration not only the 'expected' optimum catch, but also the probability of a decline in population size: management based on 'best estimates' alone may lead to significant errors in setting quotas. There are, however, probably few large mammals for which the data base is as good and even fewer populations of large mammals that are as large as the harp seal. Future monitoring of population changes and concomitant changes in physiological and population parameters promises to add very considerably to our understanding of the dynamics of populations of large mammals in general and marine mammals in particular.

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Modification of Swimming Mode and Stamina in Two Stocks of Coho Salmon (*Oncorhynchus kisutch*) by Differing Levels of Long-Term Continuous Exercise

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BESNER, M., AND L. S. SMITH. 1983. Modification of swimming mode and stamina in two stocks of coho salmon (*Oncorhynchus kisutch*) by differing levels of long-term continuous exercise. Can. J. Fish. Aquat. Sci. 40: 933–939.

Coho salmon (*Oncorhynchus kisutch*) smolts from two different stocks were exercised continuously for 40 d at water velocities of 0.2 (control), 1.0, 1.5, and 2.0 body fork lengths per second. Their critical velocities and swimming characteristics were determined using a Blazka-type respirometer–stamina swimming chamber immediately after training and after 2 mo of rest. Endurance increased in exercised fish compared with control groups and the improvement was maintained after the period of rest. Swimming modes in freshwater differed between the two stocks, and it is suggested that these were adaptations resulting from differing genetical backgrounds. Continuous moderate exercise modified swimming modes in seawater. Long-term low water velocity regimes before release in the ocean might be a profitable rearing strategy for the survival of coho salmon because it allows an economy of energy during their oceanic migrations and improves their homeodynamic capacity.

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De jeunes coho (*Oncorhynchus kisutch*) en période de smoltification provenant de deux lignées différentes furent exercés de manière continue pendant 40 jours à des vitesses de nage de 0,2 (témoins), 1,0, 1,5 et 2,0 longueurs corporelles à la fourche par seconde. Leurs vitesses critiques et leurs caractéristiques de nage furent mesurées immédiatement après la période d'entraînement et 2 mo plus tard en utilisant un tunnel d'exercice de type Blazka. Les modes natatoires en eau douce différaient chez les deux lignées et on suggère qu'ils reflétaient des adaptations résultant de bagages génétiques différents. L'exercice modéré continu a aussi modifié leur mode de nage en milieu marin. L'utilisation de régimes de nage de faible vélocité et de longue durée avant libération des saumoneaux en milieu marin pourrait être une stratégie d'élevage susceptible d'améliorer les possibilités de survie du coho car elle lui permet une économie d'énergie durant ses migrations océaniques et améliore sa capacité homéocynétique.

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ALTHOUGH it has been demonstrated that long-term continuous natatory exercise regimes for smolting Atlantic salmon (*Salmo salar*) are very efficient rearing strategies to increase the proportion of returning spawners (Wendt and Saunders 1973), little is known of the modifications produced by this type of exercise on the swimming characteristics of the fish. The purpose of this study was to measure these effects on swimming characteristics by comparing smolting coho exercised at three regimes of different current intensities with fish reared in the absence of significant water current. Comparisons were made immediately after the end of the exercising period and 2 mo later to assess the durability of these changes. Swimming characteristics were also evaluated after introduction of these fish into seawater.

Three swimming characteristics were measured. The first two are related to the strength of the tail muscles and the third reflects the overall effect on the swimming endurance capacity. Regression lines were computed from measurements of tail beat frequency as a function of water current velocity (which is also the swimming speed) and statistically compared. The distance traveled during one tail beat cycle, or stride (Wardle 1975), was derived from these regression lines and expressed as a proportion of the fish fork length (FL). Finally, we determined the 15-min critical swimming speed (15-min U_{crit}).

Materials and Methods

Two stocks of smolting coho salmon (*Oncorhynchus kisutch*) were selected from rearing tanks of the National

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Marine Fisheries Service Laboratories in Seattle. In the first experiment, 845 underyearlings (0-age) originating from the Toutle River and raised under an accelerated rearing program in Seattle (Mighell 1979) were selected according to their FL (between 6.6 and 8.6 cm). In a second experiment during the following year, 600 yearlings from Baranof Island (Alaska) raised in Seattle under a normal water temperature regime (i.e. no growth acceleration) were selected for FL between 11 and 13 cm.

Fish were held in long shallow plywood troughs (305 cm × 20 cm × 11 cm) to ensure a uniform water flow. Water flowed by gravity in four troughs in which velocity regimes were controlled by a system of valves. Water temperature was maintained at approximately 15°C (±2°C) by continuously adding fresh dechlorinated chilled city water to the system (for more details, see Besner 1980).

Experimental Design

Underyearling coho from the Toutle River were separated into four groups of 215 fish each, to be exercised at 0.2 (control group), 1.0, 1.5, and 2.0 FL/s, respectively. Water velocities were increased to their final values within 1 wk. During the following 40 d of training, water velocities were further augmented according to the average increase in body length. Fish were fed Oregon Moist Pellets once a day six times a week to satiation. After training, a small proportion of the fish were kept at minimal water velocity (0.2 FL/s) in circular tanks for 2 mo, while the majority were placed directly into seawater (28‰) in floating net pens at Manchester, Washington.

The training period for Alaska coho also lasted 40 d, and we used the same facilities as before. Because of their larger size, only 600 fish were selected and separated into four groups of 150. The experimental design was as for Toutle coho except that fish were fed to satiation twice a day.

Definitions

The specific swimming speed (U/L) is the proportion of the fork length of a fish traveled in 1 s (FL/s). Because all fish obstructed more than 10% of the cross-sectional area of their swimming compartment, U/L was corrected for the effects of solid blocking using the formula of Bell and Terhune (1970):

$$V_f = V_t (1 + e_s)$$

where V_f = effective free stream velocity about the fish, $V_f = U/L$ (in FL/s) when the fish maintain position as they did in the swimming apparatus, V_t = average velocity in the empty test section, and e_s = fractional error in V_t due to blockage (this error depends on the cross-sectional area of the fish and was calculated for each fish tested).

The term "swimming mode," used with the same connotations as in Smith (1982), is restricted to the statistical comparison of the tail beat frequency (TBF) as a function of V_f. It is expressed as a linear regression equation of TBF on V_f, where $V_f = U/L$. Each regression line was calculated from tail beat (TB) counts made at different velocities on many fish for each group (see below), and all observations were pooled to obtain the regression equations.

The stride length (SL) is derived from the swimming mode. It is the distance traveled during one TB cycle (Wardle 1975) (units of SL are FL/TB).

The critical swimming speed (U_{crit}) is the maximum velocity fish could maintain for a precise time period (Brett 1964). For those fish that did not fatigue at the beginning or end of the prescribed swimming period of 15 min, U_{crit} is designated as 15-min U_{crit}.

The period during which the different groups of fish were exercised will be designated "the training period."

The "control group" refers to the group of fish that received no natatory exercise during the training period. A minimal water velocity of 0.2 FL/s was flowing in the rearing trough of the control group to ensure good oxygen replenishment and elimination of metabolites from the water. However, this flow was not sufficient to orient the swimming direction of the fish.

Determination of Swimming Mode and 15-min U_{crit}

Within 4 d after their 40 d of exercise, individuals from each group of Toutle coho were tested for swimming mode and 15-min U_{crit} in a Blazka-type respirometer–stamina chamber containing 28.5 L of water. Fish were tested again after 2 mo in which there was no further exercise. Tests were performed at 15°C.

Swimming mode tests proceeded as follows. One day before testing, eight fish were chosen at random from one trough. They were anesthetized (tricaine methane sulfonate), weighed, measured, and put into individual compartments of a Blazka-type respirometer–stamina chamber (Flagg 1981). Fish remained overnight in the respirometer at minimal velocity (<0.2 FL/s). The next morning, water velocity was initially set to 1.5 FL/s, using the mean FL of the eight fish. Five minutes later, the TBF of each fish was counted. Every 15 min the water velocity was increased by 0.5 FL/s and TB were counted visually to a maximum of 3.5 FL/s. The test was stopped when three of eight fish fatigued. The time to fatigue, as well as the swimming speed, was then recorded to compute the 15-min U_{crit}.

Swimming modes of Alaska coho were measured at the end of the training period in freshwater, 5 d later in seawater, and 2 mo later in freshwater after a period without further exercise.

Testing of swimming characteristics for Alaska coho was performed in the same manner as for Toutle coho except that we used two respirometers, each containing four fish. The respirometers were identical to the one used with the Toutle coho. Tests were terminated when all fish fatigued.

Statistical Tests

Comparison of the means of 15-min U_{crit} within each group and between exercised and control groups were done using ANOVA. The test of hypothesis of equal means for a single variable, as described by Dixon and Massey (1969, p. 156–162), was used taking the 0.05 level of probability for the F ratio. Slopes and intercepts of regression lines for swimming mode were compared using the statistical

TABLE 1. Regression equations of TBF at specific swimming speeds, statistical comparisons of regression equations of exercised and control groups, and SL at three swimming speeds of Toutle and Alaska coho for all training velocities and test periods (FW, freshwater; SW, seawater).

Training velocity (FL/s)	N[a]	Regression equation $a + bx \pm 2S_{y \cdot x}$[b] (TB/min)	FL (cm)	SL (FL/TB) at: 1.5 FL/s	2.5 FL/s	3.5 FL/s
		Toutle coho				
August (FW)						
Control	61	$46 + 77\ U/L \pm 49$	11.0	0.56	0.63	0.67
1.0	59	$54 + 78\ U/L \pm 56$ (NS)	10.8	0.53	0.60	0.64
1.5	59	$43 + 84\ U/L \pm 61$*	10.8	0.54	0.60	0.63
2.0	78	$53 + 74\ U/L \pm 52$ (NS)	10.3	0.55	0.64	0.68
October (FW)						
Control	27	$44 + 76\ U/L \pm 54$	13.9	0.57	0.64	0.68
1.0	35	$53 + 72\ U/L \pm 48$ (NS)	13.4	0.56	0.65	0.69
1.5	31	$44 + 78\ U/L \pm 49$ (NS)	12.0	0.56	0.63	0.66
2.0	32	$70 + 70\ U/L \pm 48$ (NS)	12.0	0.52	0.61	0.67
		Alaska coho				
June (FW)						
Control	32	$-111 + 179\ U/L \pm 80$	14.7	0.57	0.45	0.41
1.0	36	$-109 + 174\ U/L \pm 61$ (NS)	14.0	0.60	0.46	0.42
1.5	36	$-89 + 160\ U/L \pm 60$*	14.6	0.60	0.49	0.45
2.0	40	$-88 + 157\ U/L \pm 97$*	14.9	0.61	0.49	0.46
August (FW)						
Control	24	$-136 + 184\ U/L \pm 68$	16.5	0.65	0.46	0.42
1.0	24	$-269 + 264\ U/L \pm 74$*	15.3	0.71	0.38	0.32
1.5	24	$-314 + 280\ U/L \pm 88$*	16.2	0.86	0.39	0.32
2.0	23	$-56 + 142\ U/L \pm 78$ (NS)	16.1	0.58	0.51	0.48
July (SW)						
Control	31	$-124 + 193\ U/L \pm 56$	14.5	0.55	0.42	0.38
1.0	33	$-206 + 222\ U/L \pm 77$ (NA)	14.0	0.70	0.43	0.37
1.5	29	$-188 + 202\ U/L \pm 92$ (NA)	15.4	0.78	0.47	0.41
2.0	35	$-212 + 225\ U/L \pm 86$ (NA)	14.2	0.72	0.43	0.37

[a]Number of observations considered in the calculation of the regression equation.

[b]$2S_{y \cdot x}$ = 95% confidence interval of the regression line = 2 (standard error of estimate). NS, exercised group not significantly different from control group ($P \geq 0.05$); *, significantly different ($P < 0.05$); NA, not applicable: the error terms in the two regressions did not have equal variances.

linear model described by Neter and Wasserman (1974, p. 160–165). The 95% confidence intervals of the regression lines were calculated from the standard errors of estimate (Alder and Roessler 1972, p. 205–206).

Results

SWIMMING CHARACTERISTICS IMMEDIATELY AFTER TRAINING

For Toutle coho the 1.5-FL/s group alone had a swimming mode different ($P < 0.05$) from that of the control group (Table 1). The fish in this group displayed a higher TBF for a given U/L than those of the nonexercised group. The SL in all groups increased slightly with increasing U/L from 1.5 to 3.5 FL/s and were between 0.53 and 0.68 FL/TB (Table 1). Only the fish trained at the highest velocities (1.5 and 2.0 FL/s) swam at a 15-min U_{crit} higher ($P < 0.05$) than those of the control group. The mean 15-min U_{crit} of the 1.5- and 2.0-FL/s group were 6.0 and 5.3 FL/s compared with 3.4 and 4.3 FL/s for the control and 1.0-FL/s groups, respectively (Fig. 1). Thus, long-term training did not modify the swimming mode and SL of the Toutle coho, with the exception of the 1.5-FL/s group in which the slope of the regression line was steeper and the SL slightly shorter at all velocities considered. Major changes were observed with the 15-min U_{crit} where fish exercised at 1.5 and 2.0 FL/s displayed higher ($P < 0.05$) mean 15-min U_{crit} than the nonexercised fish.

The two hardest exercised groups of Alaska coho (1.5 and 2.0 FL/s) displayed a swimming mode that differed ($P < 0.05$) from that of the control group. The slopes of the regression lines decreased with increasing training velocities (i.e. in Table 1, the lowest slope was observed for fish trained at 2.0 FL/s, while the steepest slope was observed for fish from the control group). Contrary to the situation for the Toutle coho, the SL in Alaska coho decreased with increasing

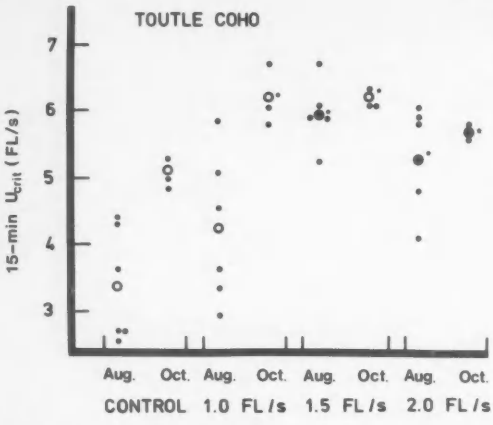

FIG. 1. The 15-min U_{crit} in freshwater of Toutle coho after 40 d of exercise (August) at different levels of exercise and 2 mo later (October) with no further exercise. ●, individual values; ○, mean; *, significant ($P < 0.05$) difference between the mean of the exercised group and that of the control group at the test period concerned.

water velocities (Table 1). The mean 15-min U_{crit} of each exercised group was higher ($P < 0.05$) than that of the control group (Fig. 2). The differences of mean 15-min U_{crit} between exercised and nonexercised fish were smaller in Alaska than in Toutle coho. The means of the 15-min U_{crit} of the control, 1.0-, 1.5-, and 2.0-FL/s groups were 3.0, 3.5, 3.3, and 3.6 FL/s, respectively. Hence, long-term training affected both the swimming mode and the 15-min U_{crit} in Alaska coho, while only the latter was modified in Toutle coho.

Swimming Characteristics 2 mo After Training

The swimming modes of all the exercised groups of Toutle coho were not statistically different ($P \geq 0.05$) from that of the control group (Table 1). The mean 15-min U_{crit} of each exercised group was higher ($P < 0.05$) than that of the control group.

During the 2 mo of rest at 0.2 FL/s following the end of the training period, the swimming modes did not change significantly within each group (Table 2) except that the 1.0-FL/s group showed a decrease ($P < 0.05$) in its regression line slope. Once again, the most important changes were observed in the mean 15-min U_{crit} (Table 2), which increased dramatically in the two groups exercised the least (the control and 1.0 FL/s groups). The increases were from 3.4 to 5.1 FL/s and from 4.3 to 6.2 FL/s in the control and 1.0-FL/s groups, respectively.

As the majority of the swimming modes in Toutle coho were not affected by long-term training, it was expected that the situation would remain the same 2 mo later. Thus, the improved 15-min U_{crit} in control and 1.0-FL/s groups is quite surprising and indicates that increase in 15-min U_{crit} does not depend only on muscular development.

The regression lines of TBF on U/L of the 1.0- and 1.5-FL/s groups of Alaska coho were steeper ($P < 0.05$) than that of the nonexercised fish (Table 1). This was a considerable change from the swimming modes observed 2 mo earlier in these groups (Tables 1 and 2). The swimming modes of the control and 2.0-FL/s groups, as with the Toutle coho, did not alter 2 mo after completion of the training period. It appears that long-term exercise positively affected (i.e. a decrease in the slope of the regression lines and an increase in the SL) the swimming mode of the Alaska coho stocks alone. However, this was a short-term modification except for the fish exercised at 2 FL/s. In the latter, the swimming mode observed at the end of the training period was maintained for 2 mo.

The means of the 15-min U_{crit} in all groups remained similar ($P \geq 0.05$) to the values observed 2 mo previously (Table 2). Contrary to the Toutle coho, no major increase was observed in the 1.0-FL/s group. The means of the 15-min U_{crit} of the control and 1.0-FL/s groups increased slightly from 3.0 to 3.3 FL/s and from 3.5 to 3.6 FL/s (Fig. 2), the final values being similar to that of the 1.5-FL/s group. We concluded that the 15-min U_{crit} did not decrease in either stock 2 mo after the end of the training period. In fact, in all groups of both stocks, there was actually an increase in the mean 15-min U_{crit}. However, this increase was only significant ($P < 0.05$) in the control and 1.0-FL/s groups of the Toutle coho. Thus, the major benefit to the 15-min U_{crit} of long-term training in both stocks was the accelerated development of the physiological mechanisms related to increase in stamina.

Swimming Characteristics of Alaska Coho After Introduction Into Seawater

The error terms in the regression equations of the trained fish did not have variances equal to those of the nonexercised fish. Consequently, no statistical comparisons were possible between the regression lines of exercised and nonexercised fish (Table 1). A similar problem occurred when swimming modes within each group for June and July were compared (Table 2). Only the 1.0- and 2.0-FL/s groups could be statistically compared, and in both, the swimming modes in seawater differed ($P < 0.05$) from those in freshwater.

An important observation was made when the SL were examined at a velocity of 1.5 FL/s (Table 1). The SL of exercised fish were longer than those of the nonexercised fish. This would allow fish with cruising speeds of 1.5 FL/s to save energy in muscular contraction (i.e. the same cruising speed would be maintained in both nonexercised and exercised fish but with a lower TBF in the latter).

Only fish exercised at 2.0 FL/s had a higher ($P < 0.05$) mean 15-min U_{crit} than that of the control group (Fig. 2). This resulted from the fact that only the control group significantly increased ($P < 0.05$) its 15-min U_{crit} during the passage from freshwater to seawater (Table 2).

Discussion

Modifications to Swimming Characteristics by Long-Term Exercise

Long-term exercise increased the strength of muscular contractions of the caudal peduncle of Alaska coho. This was

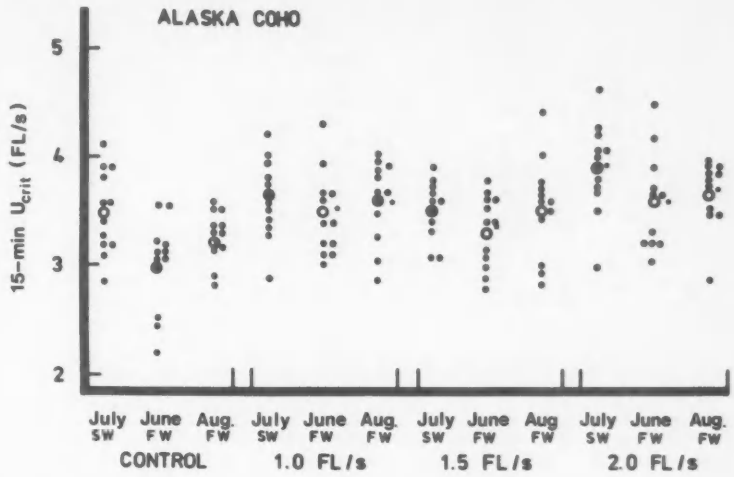

FIG. 2. The 15-min U_{crit} in both freshwater (FW) (June) and seawater (SW) (July) of Alaska coho after 40 d of exercise in freshwater and after a period of no further exercise (August). ●, individual values; ○, mean; *, significant ($P < 0.05$) difference between the mean of the exercised group and that of the control group at the test period concerned.

TABLE 2. Summary of intragroup statistical comparisons of swimming mode (regression equations of TBF vs. U/L) and of 15-min U_{crit} immediately after the end of the training period and 2 mo later; intragroup comparison of Alaska coho immediately after the end of the training period in freshwater (FW) and 5 d later in seawater (SW) (control group = 0.2 FL/s; NS, not significantly different ($P \geq 0.05$); *, significantly different ($P < 0.05$); NA, not applicable: the error terms in the two regressions did not have equal variances).

	TBF vs. U/L groups				15-min U_{crit} groups			
	0.2[a]	1.0	1.5	2.0	0.2	1.0	1.5	2.0
Toutle coho								
August vs October	NS	*	NS	NS	*	*	NS	NS
Alaska coho								
June vs August	NS	*	NA	NS	NS	NS	NS	NS
June (FW) vs July (SW)	NA	*	NA	*	*	NS	NS	NS

clearly demonstrated by the slopes of the regression lines in June (Table 1), which were lower ($P < 0.05$) for the 1.5- and 2.0-FL/s groups than for the control group. This induced longer SL in fish of these exercised groups than in nonexercised Alaska coho. In the coalfish *Gadus virens*, at 1.0 FL/s only the aerobic muscle fibers increased in diameter, while at 2.0 and 3.0 FL/s both aerobic and anaerobic muscles hypertrophied (Greer Walker 1971; Greer Walker and Pull 1973). Hudson (1973) demonstrated that electrical activity was initiated in the anaerobic muscle of the rainbow trout, *Salmo gairdneri*, at TBF between 183 and 216 TB/min. These TBF represent U/L of 1.5−2.5 FL/s in Alaska coho. Hence, long-term exercise regimes of more than 1.0 FL/s were required to develop the anaerobic mass of skeletal muscle and change the swimming modes of Alaska coho.

The swimming modes of Alaska and Toutle coho were very different. The slopes of the regression lines of the Alaska coho were much higher than those of Toutle coho. The swimming mode of Toutle coho was very similar to that found in rainbow trout by Hunter and Zweifel (1971). Differences in swimming characteristics between different stocks of rainbow trout and steelhead were observed by Tsuyuki and Williscroft (1977). Electrical activity in the anaerobic muscle of rainbow trout was found between 1.5 and 2.5 FL/s (Hudson 1973) in some cases, while in others it was not detected at velocities as high as 4.5 FL/s (Bone et al. 1978). Hence, the difference in swimming modes between Toutle and Alaska coho was probably related to their genetical stock differences.

Differences in swimming modes might necessitate different training levels. For each 1-FL/s increase in water velocity,

Toutle coho had to increase their TBF by about 75 TB/min. For the same training level, Alaska coho contracted their tail muscles with more than twice the frequency in 1 min than Toutle coho. This might explain why the swimming modes of the Toutle coho were not affected by training levels of 1.5 and 2.0 FL/s as in Alaska coho.

The mean 15-min U_{crit} was higher ($P < 0.05$) in fish exercised at 1.5 and 2.0 FL/s. This increase in stamina did not depend on the swimming mode alone, since it was observed in both Toutle and Alaska coho. Long-term natatory exercise increases the aerobic capacities of the fish and helps to maintain the blood and muscle nutrients and metabolite equilibrium. After strenuous exercise, such as in the 15-min U_{crit} test, plasma glucose concentrations are maintained at more adequate levels in trained fish, probably as a result of the effect of training on enzyme systems such as those involving the hexokinases (Hammond and Hickman 1966). In trained fish, after strenuous exercise, blood and muscle lactate are eliminated more rapidly (Wendt and Saunders 1973; Hammond and Hickman 1966; Poston et al. 1969), while muscle glycogen restoration is accelerated (Poston et al. 1969; Hochachka 1961). Long-term exercise induces an enlargement of the heart and increases concentrations of hemoglobin and myoglobin in blood and muscle, respectively (Love et al. 1977; Hochachka 1961). A major effect of long-term exercise is the development of aerobic muscle in which mitochondria are enlarged and the number and diameter of fibers are increased (Davison and Goldspink 1977, 1978). The increase in stamina observed in exercised fish of both stocks resulted from all of these effects of endurance (long-term, low-level exercise) training.

Only Alaska coho displayed a positive change of mode after training (Table 1) and it was maintained (Table 2) only by the group exercised at the highest water velocity (i.e. 2.0 FL/s) during the following 2 mo. In Alaska coho trained at 1.0 and 1.5 FL/s, the changes were negative, producing very steep regression lines (high slopes in Table 1). When SL at 1.5 FL/s are considered 2 mo after the end of the training period Alaska coho of the 1.0- and 1.5-FL/s groups had the longest SL observed at any stage of the experiment. This would favor an economy of energy in muscular contraction at low cruising speed. The sustained cruising speed for migrating coho salmon is between 0.5 and 2.9 FL/s (Ellis 1966). For fish trained at 2.0 FL/s, the economy of energy would occur at higher cruising velocities. Hence, it is possible that long-term training would favor an economy of energy at cruising speed or an increase in the speed of oceanic migration. The aerobic muscle is mainly associated with maintaining a cruising speed (Bone 1975), and its development as a result of endurance training would explain the development of the swimming modes that favor economy of energy during long-distance migrations.

The increases in the mean 15-min U_{crit} were maintained in all groups of both stocks during the 2 mo after the end of the training periods. The physiological changes mentioned earlier were not transient. The exercised fish maintained a high level of adaptability to strenuous exercise. The control and 1.0-FL/s groups of Toutle coho markedly increased their 15-min U_{crit} during the 2-mo period of rest. This resulted from their improved overall physiological status after the end of the smoltification period, when no more energy was needed for parr to smolt transformation; consequently, more "usable energy" (Schreck 1982) was available for swimming performance. Flagg (1981), using the same testing respirometer–stamina chamber, the same 15-min U_{crit} test, and the same stock at the same age and year as in these experiments, demonstrated that the mean 15-min U_{crit} decreased during the smoltification period and increased afterwards.

Modifications to Swimming Characteristics in Seawater by Long-Term Exercise

After entry into seawater all groups of exercised Alaska coho displayed a longer mean SL at 1.5 FL/s than the control group. The maximum distance traveled for a given expenditure of energy occurs when the energy utilized in propulsion is equal to the resting metabolic rate (Wiehs 1973). In rainbow trout, the velocity for which this is the case approximates 1.0 FL/s (Beamish 1978). In coho salmon, the standard metabolic rate is slightly higher (Brett and Groves 1979) and the optimum cruising speed during long-distance migration should be approximately 1.5 FL/s, if we suppose that the coho smolts migrate at a constant speed of approximately 13 nautical miles (~24 km) per day, as they do after 1 yr in seawater (Godfrey et al. 1975). Exercised fish with a SL of 0.75 FL/TB and a FL of 14.5 cm would save approximately 126 000 tail muscle contractions per day at a cruising speed of 1.5 FL/s compared with nonexercised fish of the same size with a SL of 0.55 FL/TB. This is an economy of 36% in muscular contraction. This surplus of available energy could be used to increase cruising speed or to accelerate growth rate.

All the exercised groups maintained their high mean 15-min U_{crit} (Table 2). This ability to sustain a high swimming speed would help them in pursuing prey and escaping from predators.

In mammals, highly repetitive, low-strength movements produce endurance and improve the level of activity that can be maintained at a steady state (Morehouse and Miller 1976). The cruising speed during migration of salmon depends on this homeodynamic capacity. The maintenance of high 15-min U_{crit} (endurance) over a long period of time (2 mo) indicates that the homeodynamic capacity was improved in fish through long-term low levels of exercise regimes. It can then be expected that cruising speed would be increased, as demonstrated by their longer stride lengths at 1.5 FL/s. In Sweden, the percentage of returning Atlantic salmon spawners was doubled by using training velocities of over 2.0 FL/s for 2–12 mo before release into the ocean (Wendt and Saunders 1973). The training level to improve the homeodynamic capacity in coho salmon is probably over 1.0 FL/s and depends on the stocks concerned.

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Photoperiodic and Ecdysial Control of Vitellogenesis in Lobsters (*Homarus*) (Decapoda, Nephropidae)

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NELSON, K., D. HEDGECOCK, AND W. BORGESON. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). Can. J. Fish. Aquat. Sci. 40: 940–947.

The timing of molts and of subsequent egg extrusion by female American lobsters (*Homarus americanus*) in the laboratory under near-ambient conditions at Bodega Bay suggested that final vitellogenesis was initiated only during the months between the vernal and autumnal equinoxes. In an experiment, the change from short-day (LD 8:16) to long-day (LD 16:8) photoperiod (long-day onset, LDO) began a 120-d period during which vitellogenesis could be initiated. Molting within this 120-d period was associated with a delay of as much as 80 d in the time of subsequent extrusion.

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Le moment de la mue et de l'expulsion subséquente des oeufs chez des homards femelles américains (*Homarus americanus*) en laboratoire, dans des conditions à peu près ambiantes à Bodega Bay, donne à penser que la vitellogénèse finale n'est déclenchée que durant les mois compris entre les équinoxes de printemps et d'automne. Au cours d'une expérience, le passage d'une photopériode de jour court (8:16) à un jour long (16:8) marqua le début d'une période de 120 jours au cours de laquelle la vitellogénèse finale a pu être déclenchée. La mue, durant cette période de 120 jours, a été associée à un délai aussi long que 80 jours de l'expulsion subséquente des oeufs.

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THE interactions between reproductive and growth processes in Crustacea have long been the subject of speculation and confusion (e.g. Adiyodi and Adiyodi 1970). Cyclic growth and reproduction both make demands upon the organism's energy resources, which must somehow be reconciled. In addition, crustaceans that brood their eggs must ensure that premature ecdysis does not cause the loss of the clutch. How all this is accomplished is unknown (also see Swartz 1978).

The reproductive cycle of female American lobsters (*Homarus americanus*) takes 2 yr in nature (Herrick 1895, 1902, 1909). In the "typical" cycle, the female molts and mates in late summer or early autumn, soon after hatching her previous brood. The eggs are extruded in the following summer and are carried on the pleopods through the next winter until they hatch in the following late spring or summer. The cycle then repeats. The seasonal nature of the events in this complex cycle suggests control by photoperiod or temperature or both, but evidence heretofore has been lacking (for a review, see Aiken and Waddy 1980). In particular, the physiological need for a 2-yr reproductive cycle remains a mystery.

We report here the results of observations indicating photoperiodic control of the physiological events leading to extrusion and of an experiment confirming this. Other evidence is presented concerning interactions of the female lobster's reproductive cycle with her molting cycle.

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Materials and Methods

A cumulative day calendar, starting with Jan. 1 (followed by the year where necessary), is used in this paper to facilitate statistical analyses. Traditional dates are given where necessary for orientation. Month number may be obtained approximately by dividing the cumulative date by 30. Unless otherwise indicated, all estimates of variation are standard errors of the means. All F ratios are derived from one-way ANOVA.

PRELIMINARY OBSERVATIONS ON THE TIMING OF MOLTING AND EXTRUSION

Two large, semirecirculating seawater systems — an adult holding system of racked troughs and an experimental broodstock-holding facility consisting of eight batteries of nine 115-L compartments each — have been described previously (Hand et al. 1977; Hedgecock et al. 1978).

Since 1973, ovigerous lobsters (*H. americanus*) have been imported to Bodega Bay several times each year from Martha's Vineyard to supply larvae for experiments on growth and nutrition. When their eggs had hatched, many of these females were maintained in individual compartments in

our adult- and broodstock-holding systems under uncontrolled or ambient photoperiods (until late 1978) and near-ambient seawater temperature conditions (generally 1−3°C higher than the prevailing coastal water surface temperature). Ambient surface temperature at Bodega Bay peaks in the late fall at 15−16°C and reaches a minimum of 7−9°C for a variable period in the spring during the coastal upwelling period. Detailed temperature records are available from our archives.

All animals were maintained on a varied diet (fish, squid, mussels, shrimp, compounded diet) on a basis of approximately 2½% body weight per day. Molts were recorded on a daily, and presence of eggs on a weekly, schedule. All "extrusion dates" mentioned in this paper thus refer to the dates when eggs were first noticed. Molted females were generally mated, often to a *Homarus gammarus* male, as we were interested in obtaining hybrid progenies. The male was placed with the female and her exuvia and either observed until mating was seen or left overnight with her. Presence or absence of an externally visible sperm mass in the female's annulus was noted.

Photoperiod Experiment

This experiment was designed to determine whether and how accurately the date of extrusion was regulated by the date of onset of long days (LDO) and to study the modification of the timing of extrusion by the occurrence of a molt following LDO.

Fifty-four compartments of our experimental broodstock system were fitted with fiber-optic lighting and light-tight covers (Fig. 1). Compartments and covers were of marine plywood, coated with clear polyester resin. Light leaks were sealed with black silicone caulking. For each group of 18 compartments, a 3-A, type H2 quartz iodine headlamp (Cibie Projecteurs, 93 Bobigny, France) with a 12-V DC power supply switched from a dairy timer was trained on an array of No. 16A01 convex-lens input modules (Prince Products, Inc., Brooklyn, NY, 11212 USA). From each input lens a black-coated, 1.8-m-long, 3.3-mm-diameter No. 1610 CROFON light guide (DuPont Co.) led to a No. 16B01 convex-lens output module (Prince Products, Inc.) mounted in the wall of a compartment. Output intensity in air parallel to the axis of one output module was measured with a ISCO model SR spectroradiometer at 25-nm intervals; it rose approximately linearly with wavelength from 0 $\mu W \cdot nm^{-1}$ at 450 nm to 0.56 $\mu W \cdot nm^{-1}$ at 700 nm and fell sharply to 0.21 $\mu W \cdot nm^{-1}$ at 725 nm. Intensity at 525 nm (the peak of the difference spectrum for lobster rhodopsin; Kennedy and Bruno 1961) was 0.24 $\mu W \cdot nm^{-1}$ and total output intensity was on the order of 100 μW.

On day 354/79 (Dec. 20), 87 wild-caught adult *H. americanus* females, carapace lengths 80.5−89.0 mm, were obtained from Martha's Vineyard and placed in two 2000-L holding tanks with light-tight covers. Here, the animals were exposed to dim aquarium room illumination from 08:30 to 16:30 daily by partial lifting of the covers (LD 8:16).

Fifty-four females that met all of the following criteria were selected for use in the experiment.

1) Undamaged; ratio of maximum abdominal tergal width to carapace length from orbit at least 0.62.
2) Ovary, as judged by candling (Hedgecock et al. 1978) at least at 1.0 on a scale of 0−4.
3) Serum concentration of female−specific protein (precursor of egg protein) at least 0.2 $mg \cdot mL^{-1}$ on day 093/80 as measured by rocket immunoelectrophoresis (Heyer et al., unpublished data; description of technique available upon request).
4) Absence of third component on rocket immunoelectropherogram (signifying resorbing ovary; Heyer et al., unpublished data).

These criteria were chosen on the basis of previous (unpublished) work as indicating ovaries competent to undergo final development (but which ordinarily would not do so without the stimulus of LDO, as we shall show).

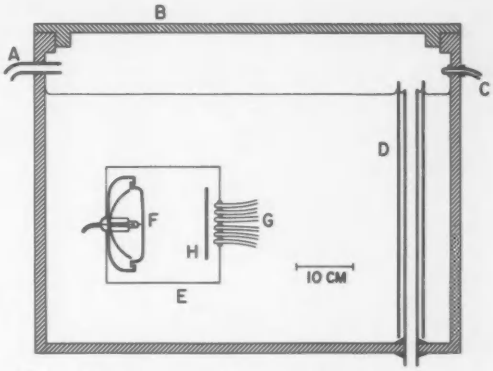

FIG. 1. Schematic cross-section of experimental broodstock compartment showing light-proof water inlet (A), light-tight cover (B), light guide and output module (not to scale) (C), and standpipe with sleeve (D). Inset: headlamp box (one for each 18 compartments) showing light-tight box (E), quartz iodine headlamp (F), input modules and light guides (not to scale) (G), and etched glass screen (H).

On day 108/80 (Apr. 17), the 54 experimental subjects were distributed randomly in compartments under three photoperiod regimes as follows.

Condition C-1 (early LDO):	LD 8:16 (lights on at 08:30 in all conditions) until 108/80, LD 16:8 (lights on at 04:30 in all conditions) thereafter;
Condition C-2 (middle LDO):	LD 8:16 until 136/80 (May 15), LD 16:8 thereafter;
Condition C-3 (late LDO):	LD 8:16 until 164/80 (June 12), LD 16:8 thereafter.

Temperature was not controlled. Its average level, generally several degrees above Bodega Bay ambient seawater temperature, changed several times during the experiment, as follows (mean followed by standard deviation):

Dec. 20−Mar. 20: 14.4 ± 0.7°C;
Mar. 21−May 7, May 16−July 9: 13.0 ± 0.9°C;
May 8−May 15: 9.8 ± 0.3°C;
July 10−Nov. 11: 16.8 ± 0.8°C;

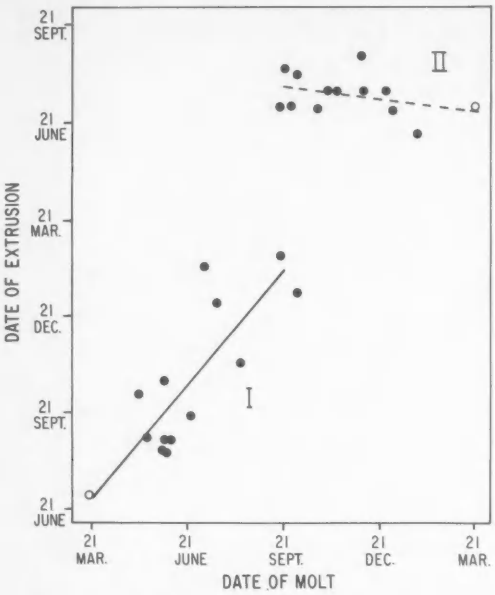

FIG. 2. Relationship of extrusion date to ovulatory molt date at different times of the year under uncontrolled photoperiod. I, molts that are followed shortly by extrusions: regression of date of extrusion y upon date of preceding molt x after 365 is added to following-year extrusion dates: $y = 93.81 + 1.135x$; $r = 0.82$; 12 df; $P < 0.01$. II, molts in which extrusion is postponed until the following spring: $y = 192.2\text{-}0.127x$ after subtracting 365 from preceding-year molt dates; $r = -0.37$; df 11; $P > 0.05$. Open circle: an ovulatory molt on Mar. 20 (day 079), classified into both groups for the purpose of regression.

Nov. 12–Dec. 13: 15.0 ± 0.5°C;
Dec. 14–Dec. 23: 12.7 ± 1.2°C.

During the colder periods from May 8 to 15 (days 129–136) and Dec. 14 to 23, recirculation pump failures necessitated the use of flow-through seawater at near-ambient temperature. Subjects were fed coarse-chopped whole squid and whole shrimp on alternate days on a basis of $2\frac{1}{2}$% body weight per day. The experiment was terminated on day 358/80 (Dec. 23). Following extrusion, or after Dec. 23 in the case of animals that had not extruded, subjects were transferred to the adult holding system (near-ambient temperatures, LD 15:9) but were monitored routinely for molts and presence of eggs until their following molt. All matings prior to the end of the experiment were to *H. gammarus* males.

Results

Preliminary Observations on the Timing of Molting and Extrusion

During the years 1974–78 female *H. americanus*, most of which were ovigerous, were brought from Martha's Vineyard into our laboratory and held under ambient lighting conditions. They extruded eggs on 27 occasions, mostly after the second or later postcapture molt; i.e. the female had been in the laboratory at least a year. Molts followed by egg extrusion ("fertile" or "ovulatory" molts) could occur any time of year but were infrequent during late winter and early spring (Fig. 2).

Extrusions were similarly absent during late winter and early spring and their timing was related to the timing of the preceding molt, in a peculiar way. If the ovulatory molt occurred between the vernal and autumnal equinoxes, extrusion followed on the average in about 4 mo (Fig. 2, group I). But if the ovulatory molt occurred between the autumnal and vernal equinoxes, extrusion was delayed until approximately 4 mo after the latter date. Its occurrence then did not depend upon the date of the preceding molt (Fig. 2, group II). Ovulatory molts on or near the autumnal equinox (days 260–276 or Sept. 17–Oct. 3; Fig. 2) were followed by extrusions either approximately 120 d or approximately 300 d later and were thus easily classifiable into either group I or II. One isolated ovulatory molt on day 079 (Mar. 20, the day before the vernal equinox) appeared to belong equally to both the spring–summer group I and the fall–winter group II and was classified with each for the purpose of regression (open circles in Fig. 2).

Effect of LDO on Timing of Molting

The first molt in the photoperiod experiment was recorded 62 d after the experiment began; thus, no molts were recorded prior to LDO. The single mode of the summed initial molt date distribution (days 220–230; Fig. 3A) is near the median (day 223 or Aug. 10) and mean (day 236.8 ± 45.4 d SD).

LDO seemed to affect neither the average time of molting nor its variability, for the means of the molt date distributions in each of the three photoperiod conditions are similar (Table 1, line 1; $F = 0.43$; df 2, 37; $P > 0.5$), as are their standard deviations (50.6, 41.9, and 45.9 d for conditions C-1, C-2, and C-3, respectively).

Effect of LDO on Timing of Extrusion

The distribution of dates of extrusion appears to be highly dependent upon the date of LDO. One-way ANOVA of extrusion dates yields a highly significant between-photoperiod condition F ratio (Table 1, line 3; $F = 12.20$; df 2, 31; $P \ll 0.001$). The mean LDO–extrusion intervals under the three conditions are similar (Table 1, line 4; $F = 0.28$; df 2, 31; $P > 0.5$), as are their standard deviations.

The Effect of Molting on the Timing of Extrusion

For this analysis we must distinguish between group MM, "molt–molt" animals for which complete anovulatory molt cycles were recorded following LDO, group MEM, "molt–extrusion–molt" animals for which complete ovulatory molt cycles were recorded, and group EM, animals that extruded prior to their first molt in the experiment. For three additional animals, data were missing due to death or incomplete records.

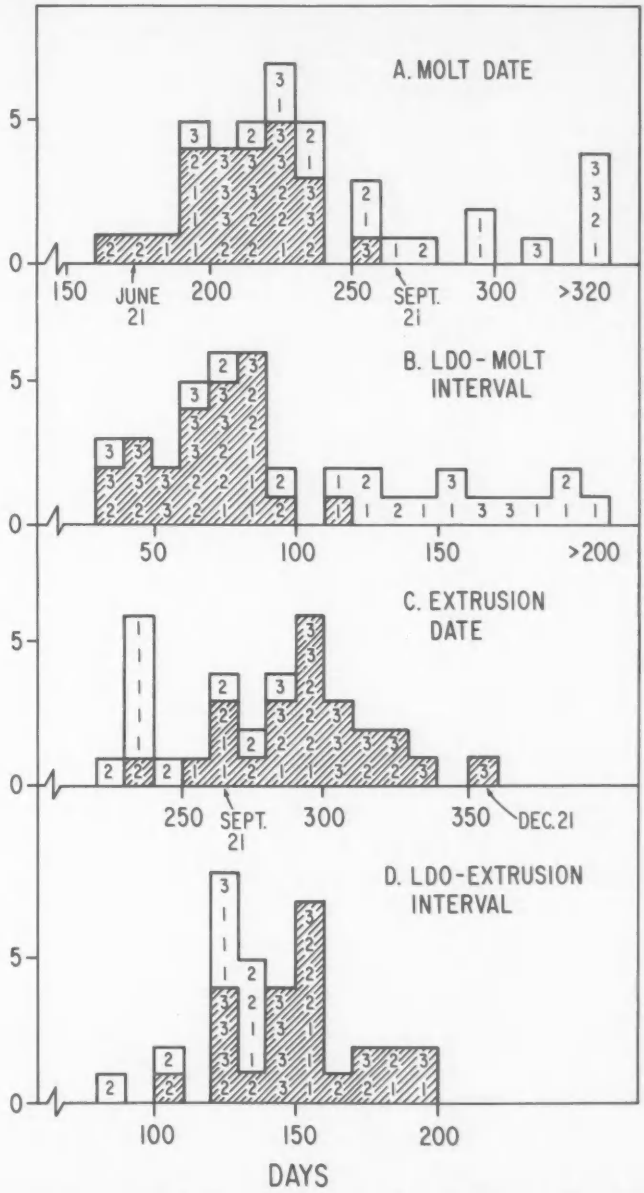

FIG. 3. (A) Frequency histogram of initial molt date (first molt by an experimental animal, not preceded by extrusion). Hachures, ovulatory molts (i.e. those followed by an extrusion, group MEM); open, anovulatory molts (i.e. those followed by another molt, group MM). Numbers refer to photoperiod conditions C-1 to C-3. (B) Frequency histogram of LDO−molt interval. Legend as in Fig. 3A. (C) Frequency histogram of extrusion date. Hachures, extrusions preceded during experiment by molt (group MEM); open, extrusion not preceded by molt (group EM). Numbers refer to photoperiod conditions C-1 to C-3. (D) Frequency histogram of LDO−extrusion interval. Legend as in Fig. 3C.

TABLE 1. Summary statistics (numbers, means, and standard errors) from photoperiod experiment. LDO, long-day onset date. Initial molt = first molt by an animal in experiment not preceded by extrusion. Group MM, "molt−molt" animals for which complete anovulatory molt cycles were recorded; group MEM, "molt−extrude−molt" animals for which complete ovulatory molt cycles were recorded; group EM, "extrude−molt" animals that extruded prior to their first molt in the experiment.

	C-1 (LDO 108)	C-2 (LDO 136)	C-3 (LDO 164)
A. All initial molts	$N = 12$	$N = 14$	$N = 15$
1. Date of molt	241.8±14.6	226.2±11.2	242.6±11.8
2. LDO−molt interval	133.8 d	90.2 d	78.6 d
B. All extrusions	$N = 10$	$N = 13$	$N = 11$
3. Date of extrusion	255.8±7.7	276.2±8.0	309.6±6.5
4. LDO−extrusion interval	147.8 d	140.2 d	145.6 d
C. Group MM	$N = 7$	$N = 5$	$N = 5$
5. Date of initial molt	273.1±16.3	262.0±20.7	281.0±28.4
6. LDO−molt interval	165.1 d	126.0 d	117 d
D. Group MEM	$N = 5$	$N = 9$	$N = 10$
7. Date of initial molt	198.2±6.4	206.3±7.0	223.4±5.0
8. LDO−molt interval	90.2 d	70.33 d	59.4 d
9. Date of extrusion	276.2±7.6	287.0±8.4	311.9±6.7
10. Molt−extrusion interval	78.0±7.6 d	80.7±7.1 d	88.5±4.8 d
11. LDO−extrusion interval	168.2 d	151.0 d	147.9 d
12. Percent of extruders	50	69	91
E. Group EM	$N = 5$	$N = 4$	$N = 1$
13. Date of extrusion	235.4±1.8	251.8±10.7	287
14. LDO−extrusion interval	127.4 d	115.8 d	123 d

Irrespective of photoperiod regime, 85% of females that molted within 100 d following LDO subsequently extruded, whereas no molts occurring more than 120 d after LDO were followed by extrusion (Fig. 3B). In contrast with the averages for all molts (Table 1, line 1), the mean date of those molts followed by extrusions paradoxically increased between conditions C-1 and C-3 (Table 1, group MEM, line 7; $F = 4.02$; df 2, 21; $P < 0.05$).

In this experiment, when extrusion occurred following a recent molt, its timing appeared to depend directly upon the date of the molt and only indirectly therefore upon the date of LDO. LDO date seemed to influence the average date of extrusions following molts only by virtue of its selective effect upon the distribution of the dates of those molts. If extrusion followed molting, it did so after an average molt−extrusion interval of about 80 d independently of date of LDO (Table 1, line 10; $F = 0.73$; df 2, 21; $P > 0.5$; see also Fig. 4). As a result, group MEM extrusions were delayed relative to group EM extrusions (Fig. 3D; Fig. 4; Table 1, compare lines 9 and 11 with lines 13 and 14). Because in these MEM extrusions the date of extrusion is the sum of the date of molt and the molt−extrusion interval, the average date of extrusion following a molt (Table 1, line 9) increases between photoperiod condition C-1 and C-3, parallel to the increase in average ovulatory molt date (Table 1, line 7). This difference in dates of extrusion following molts between the three conditions of LDO, although smaller than that for all extruders (Table 1, compare line 9 and line 3), is still significant ($F = 5.30$; df 2, 21; $P < 0.02$).

Discussion

The most significant findings of this study are that following LDO there is a period of 100−120 d during which the events leading to egg extrusion may be initiated (Fig. 3) and that the events of premolt may delay their onset (Fig. 4).

After the 120-d post-LDO period elapses, a period of short days is needed by nearly all *H. americanus* females before long-day lengths can again stimulate vitellogenesis (unpublished observations). Thus, either it is not a matter of a critical day-length being required to induce reproductive processes such as in other arthropods (Lees 1960) or else the mechanism that is sensitive to the critical day length must be reset by short days once the 120-d reproduction-initiation period has elapsed. Approximately the opposite relationship exists in *Gammarus lawrencianus*: termination of both the reproductive phase and, 3 mo later, the resting phase may depend upon the change from long days to short (Steele 1981). Dependence of reproductive processes upon critical daylength duration near 12 h has been reported for several nondecapod, freshwater, estuarine, and terrestrial Crustacea (Stross and Hill 1968; de March 1977; Bulnheim 1978; McQueen and

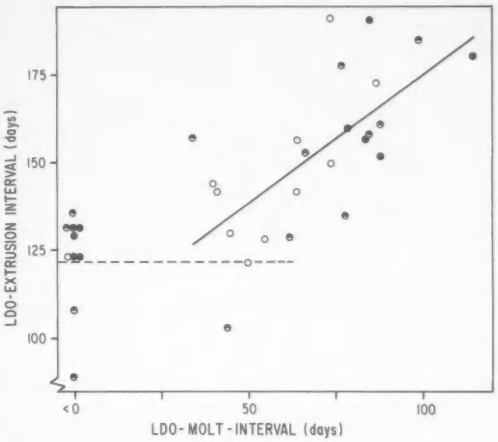

FIG. 4. LDO−extrusion interval (ordinate) as a function of LDO−molt interval (abscissa). Extrusions not preceded during experiment by molt (group EM) are included above "<0." Solid circles, photoperiod condition C-1; half-filled circles, C-2; open circles, C-3. Solid regression line is for LDO−molt intervals greater than 30 d ($y = 102.3 + 0.729x$; $r = 0.666$; df 22; $P < 0.001$). Broken horizontal line represents the function $y = 122.3$ d, the mean LDO−extrusion interval for the group EM animals.

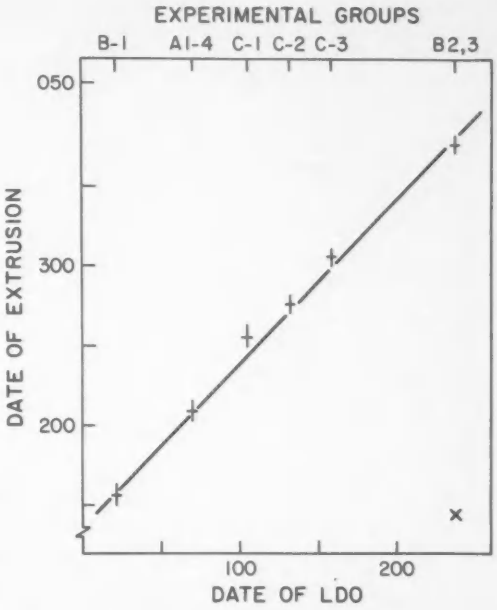

FIG. 5. Mean and two standard errors of date of extrusion (ordinate) as a function of date of LDO (abscissa) at different times of the year from several experiments (unpublished results). A1−4, extrusions under four temperature regimes (cold period variously ending on day 026, 073, or 120); all with LD 8:16 until day 073 (Mar. 14), LD 16:8 thereafter. All cold-treatment groups had similar mean dates of extrusion; only the grand mean is given here ($N = 18$). B1, LD 8:16 until day 026 (Jan. 26), LD 16:8 thereafter; near-ambient temperatures ($N = 5$). B2, LD 8:16 until day 240 (Aug. 28), LD 16:8 thereafter. B3, LD 2:22 until day 240, LD 16:8 thereafter; both with near-ambient temperatures. Photoperiod regimes B2 and B3 have identical LDO's and similar mean LDO−extrusion intervals, and the results are combined as with A1−4 ($N = 4$ and 6, respectively). ×, an earlier extruder in group B2, not included in mean. C-1 to C-3, the groups of the present experiment (Table 1, line 3). Solid line, regression of date of extrusion y on date of LDO x for all individuals in experiments A−C except the early extruder (×) in group B2: $y = 138.4 + 1.012x$ (with 365 added to following year dates); $r^2 = 0.889$; $N = 75$.

Steel 1980) but not for decapods or marine crustacea, and there is some question as to its generality (Steele et al. 1977).

European lobsters (*H. gammarus*) often extrude in the laboratory after each molt without benefit of LDO, in either short days or continuous long days (unpublished observations). Although typically biennial spawners, *H. gammarus* females in the wild apparently sometimes extrude annually especially when transplanted to the inverted seasons of New Zealand (references in Herrick 1909). In crayfish, ovarian maturation and/or stabilization may require a period of short day-lengths, but the role of photoperiod in their reproductive processes appears otherwise dissimilar to the American lobster (*Orconectes*, Stephens 1952; Aiken 1969; Armitage et al. 1973; *Cambarellus shufeldti*, Lowe 1961; *Procambarus simulans*, Perryman 1969). The existence of a reproductive period whose dates of termination as well as initiation can be shown to be dependent upon LDO seems thus far to be unique to the American lobster.

It is possible that the reproductive period in the experimental lobsters was terminated by an endogenous rhythm, preset before they were brought into the laboratory, but with the date of cutoff perhaps modulated by date of LDO. But pilot experiments with LDO at days 026, 073, and 240 resulted in similar average LDO−extrusion intervals (Fig. 5) and final ovulatory molt dates 91, 101, and 78 d post-LDO, respectively (unpublished observations). Thus, both the timing of the beginning and the timing of the end of the period during which final vitellogenesis may be initiated appear to be functions of the date of LDO.

The termination of this period may result from interference of premolt events with final vitellogenesis. If the molt precedes LDO, or occurs within 40 d after it, there is no interference, and extrusion occurs on schedule. If the molt occurs between about 40 and 120 d post-LDO, premolt events apparently interfere with final vitellogenesis, and extrusion is postponed (Fig. 4). Study of the fate of extrusions in this and other experiments suggests that clutch size and probability of retention are directly correlated with the duration of the molt−extrusion interval, again indicating interference of premolt events with normal vitellogenesis (unpublished results). And if the molt is to occur more than 100−120 d post-LDO, the processes of premolt may cause an already-initiated final vitellogenesis to abort completely. Reinitiation apparently must then await the stimulus of another LDO.

Such major interference with final vitellogenesis would be

expected with molts falling between 100 and 180 d post-LDO, in good agreement with the anovulatory molts of Fig. 3B. Aiken (1980) suggested that "active premolt (irreversible)" begins with stage D_1 after approximately 82% of the molt cycle has elapsed. Ecdysteroid titers begin to rise in stage D_0 after approximately 83% of the molt cycle, according to Chang and Bruce (1980). This would occur about 60 d prior to the molt in our subjects. Final vitellogenesis appears to begin approximately 40 d post-LDO, when molts begin to delay extrusion (Fig. 4), and to last about 80 d, the duration of the molt−extrusion interval. Thus, events preceding molts occurring 100−180 d post-LDO should overlap temporally with already-initiated final vitellogeneses. The decision, "growth or reproduction?," would in these cases be decided in favor of the former process, now irreversible.

Whatever the origin of the 120-d post-LDO cutoff of ovulatory molts, it accounts for the paradoxical result that, whereas date of molt in general seemed independent of date of LDO, date of ovulatory molt did not (Table 1, line 7). As date of LDO increases, more and more molt dates "sampled" from the summed distribution (Fig. 3A) are within the 120-d limit. Accordingly, from condition C-1 to condition C-3 a greater and greater percentage of extrusions follows occurrence of molt (Table 1, line 12), the mean of the ovulatory molt dates increases (Table 1, line 7), but the mean LDO−molt interval decreases (Table 1, line 8; $F = 5.02$; df 2, 21; $P < 0.02$). With a relatively constant molt−extrusion interval, the average extrusion date in group MEM increases and the average LDO−extrusion interval decreases in corresponding fashion (Table 1, lines 9 and 11, respectively).

Phase relationships between molting, reproduction, and LDO are no doubt quite different in the field. We are unsure of the effective time of LDO in New England inshore waters, but we will assume it to be near the vernal equinox, where the two regression lines in Fig. 2 intersect (day 078, Mar. 19). Our experimental LDO's for conditions C-1, C-2, and C-3 were, respectively, 28, 56, and 84 d later than the vernal equinox, and our winter temperatures were much warmer than in New England inshore waters and may have accelerated the molt cycle. Both factors should result in many more molts being included within the 120-d post-LDO period of vitellogenic initiation than would occur in nature.

It is clear that the natural cycle is vastly modified in our laboratory by the local northern California temperature regime. In one pilot experiment we found little effect of different durations of water temperatures as low as 6°C on the temporal relationships of extrusion to molting and LDO (unpublished results; Fig. 5, groups A1−4). However, temperatures much below 6°C appear completely to suppress both molting (Aiken and Waddy 1976) and vitellogenesis (D. E. Aiken, personal communication). The 9-mo molt cycles of our laboratory lobsters probably correspond to annual cycles in the extremely seasonal temperature regime of New England inshore waters, and winter suppression of embryo development increases the developmental time of the eggs from 4−5 mo in the laboratory at 17−20°C to 11−12 mo in the field (Perkins 1972).

Nevertheless, interference of molting with reproduction, and the 120-d post-LDO cutoff in ovulatory molts, may play a crucial role in the normal 2-yr cycle of the American lobster. If a newly matured female (Adult-I year) molts before, e.g., late July, she may be able to extrude the same autumn (Aiken and Waddy 1976). If she is a female already carrying eggs, she must hatch them first. Soon after hatching her previous brood, she molts and mates, but the critical post-LDO period allowing prompt vitellogenesis has passed. She now must await the stimulus of LDO the following spring for another chance. After LDO she may or may not molt again before extruding. After extrusion, the eggs must be carried through the next winter and spring until they hatch the following summer, and thus, 2 yr will have elapsed since the previous hatch.

Acknowledgments

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Growth Rate and Survival in Pure Population Matings and Crosses of the Oyster *Crassostrea virginica*

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Phenotypic differences were observed among pure population matings and crosses grown in two natural environments for the following characters: larval shell length, juvenile and adult shell length, weight, and survival at different times. For growth characters, the phenotypic variability between locations was greater than the variability among genetic groups within locations; however, the magnitude of the differences depended on the locality. The crosses exhibited higher survival than pure population matings, and locality had no effect on survival. In growth and survival, some crosses deviated positively from the mean of the parental populations. This may be a manifestation of heterosis. The genetic enhancement of commercially important characters in shellfish will eventually require the formation of a closed breeding unit with a broad genetic base for domestication and selection. It is recommended that an evaluation of natural populations as outlined in this study is a necessary prerequisite to achieve this objective.

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Dans des accouplements au sein et entre des populations pures élevés dans deux environnements naturels, on a observé des différences phénotypiques des caractères suivants : longueur de la coquille larvaire, longueur de la coquille des juvéniles et des adultes, poids et survie à différentes époques. Pour ce qui est des caractères de croissance, la variabilité phénotypique entre localités est supérieure à celle qu'on observe entre groupes génétiques dans une même localité. Cependant, l'ampleur des différences dépend de la localité. Les descendants de croisements montrent une survie supérieure à celle des descendants de populations pures, et la localité n'a pas d'influence sur la survie. Sous le rapport de la croissance et de la survie, certains croisements montrent une déviation positive de la moyenne des populations parentales. Ceci peut être une manifestation d'hétérosis. La valorisation génétique de caractères d'importance commerciale chez les mollusques nécessitera éventuellement la formation d'une unité reproductrice close à large base génétique à des fins de domestication et de sélection. Nous recommandons l'évaluation des populations naturelles, telle que décrite dans la présente étude, comme condition essentielle de succès.

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GENOTYPE is an important determinant of larval, juvenile, and adult growth rate and survival. The importance of the genotypic contribution to the phenotypic differences between individuals has been evaluated from (1) different populations of oysters grown in the same environments (Newkirk and Haley 1977), (2) estimates of additive and dominance genetic components in half-sib and full-sib analyses (see Newkirk 1980), (3) differential weight at 1 yr of electrophoretically characterized genotypes (Zouros et al. 1980), and (4) positive response to directional selection (Newkirk 1980). The environment also plays an important role in larval growth (Newkirk 1978), larval survival (Newkirk and Waugh 1980), and juvenile growth performance (Epifanio 1979).

Geographically separated stocks of oysters have been found to show differential resistance to the parasite, *Haplosporidium nelsoni*; Haskin et al. (1966) also commented on the potential value of the crosses. In larval growth rate and survival, Newkirk (1978) observed genetic differences between populations; however, the relative differences were dependent on the environment. The investigation of population crosses is important also and provides a measure of heterosis. Newkirk (1978) observed some crosses to be superior to the pure matings in larval characters but different genetic groups were superior at different salinities. Singh and Zouros (1978) and Zouros et al. (1980) established a strong positive cor-

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relation between the degree of heterozygosity and weight at 1 yr; hence, population crosses could lead to increased growth performance.

Even in the absence of heterosis, one would still want to initiate a breeding program with a combination of populations to provide a broad genetic base. Doolittle and Wilson (1981) found that selection from a cross stock of mice gave a greater response for traits characterized by additive gene action than does crossing from selected lines. Although these observations indicate that while the choice of oyster populations known to be superior and the crossing of these populations may provide substantial enhancement of desired larval and juvenile characteristics, the evaluation of the oyster genetic resource has been generally neglected. The selection of parents from geographically separated stocks is no guarantee of genetic uniqueness (Wilkins 1975) although one should recognize and utilize the inevitable genetic differentiation present in geographically isolated populations (Wright 1977). This evaluation of oyster populations is especially important in identifying superior stocks that may eventually contribute to the breeding stock.

The present work reports on pure matings and crosses of the American oyster, *Crassostrea virginica* (Gmelin), raised to marketable size in two natural environments to evaluate the genotypic, environmental, and genotype location contribution in various traits of commerical interest.

Materials and Methods

Experimental Group Management

A random sample of 100 adult oysters (6−9 cm) was obtained from each of six geographically separated river estuaries (Miscou (Msc), St-Simon (Sim), Miramichi (M), Bouctouche (B), Richiboucto (R), and Shemogue (S)) of New Brunswick, Canada, in May 1977. We induced gonadal maturation by placing them in 18°C filtered running seawater and feeding a mixed algal diet of *Phaeodactylum tricornutum* (Buhlin), *Thalassiosira pseudonana* (Hustedt) Haslean Heindal clone 3H, and *Isochrysis galbana* (Parke). About 40 oysters from each population were placed in a separate tray filled with UV-sterilized filtered seawater. Frequent alternation of cold (16°C) and warm (30°C) seawater was usually successful in inducing spawning. Additional stimulation was provided by adding freshly stripped gametes to the spawning tray. A successful spawner was first rinsed in seawater to remove potential contaminants and then transferred to a 2-L beaker. A sample of eggs was observed for accidental fertilizations at least 50 min after completion of spawning; any sign of contamination led to the elimination of these eggs from the study.

Experimental Design

The laboratory space available imposed a constraint on the experimental design; only six lines could be reared at a given time. The six populations were arbitrarily divided into two groups: M, B, and S and Msc, Sim, and R, respectively, and only one group of three populations was used at one time. Thus, in the first spawning (late June), using populations M, B, and S, three pure population matings and three population crosses were produced as follows. The eggs collected from all females of population M were pooled, subsequently apportioned into three subsamples, and fertilized by equal volume of sperm from populations M, B, and S, respectively. Eggs from females of population B and S were treated similarly. Eighteen individuals from Miramichi, 10 from Bouctouche, and 9 from Shemogue contributed to the genetic groups. Reciprocal crosses were pooled giving three crosses, M × B (♂B × ♀M + ♂M × ♀B), M × S (♂S × ♀M + ♂M × ♀S), and B × S (♂S × ♀B + ♂B × ♀S) in addition to the three within-population crosses of M (♂M × ♀M), B (♂B × ♀B), and S (♂S × ♀S). The same procedure was repeated for the crosses of Msc, Sim, and R populations (early August) but one of the pooled crosses, Msc × R, was not successful. In this latter cross, fertilization was apparent based on early cleavage observations; therefore, the loss is attributed to failure of these stages to grow and develop to the straight-hinge larval stage.

Developing embryos from each line were transferred to separate 400-L conical tanks and reared at a density of 5−8 larvae/mL and a temperature of 26°C. The feeding regime consisted of a mixture of *Isochrysis* and *Thalassiosira* (3:1) for the 1st wk of larval growth at a concentration of 40 000 cells/mL and at a ratio of 1:1 for the subsequent weeks at 85 000 cells/mL.

Towards the end of the larval period (approximately 12 d), 100 scallop shells were suspended in each tank to provide a substrate for metamorphosis. Every second day, the shells were replaced with 100 new ones as a means of controlling density of settlement. Adequate distance between metamorphosed larvae was insured by random culling. The newly settled oysters were allowed to grow in the hatchery to a size of 5−7 mm, and then half of the scallop shells from each line and setting date were randomly transferred to each of two growing areas, Shippagan and Richiboucto, New Brunswick.

In May 1978, at each growing site, individual oysters were separated and each oyster was labeled with a unique number so that individual life history could be recorded. These labeled oysters were then reared communally in floating trays at a density of 1/45 cm^2. Juveniles from the second spawning group, Miscou, St-Simon, and Richiboucto, with their respective crosses failed to withstand the 1977−78 winter conditions. Similar mass mortality was observed in the natural spatfall, which set late that year, and is presumably related to insufficient size prior to onset of winter conditions.

Data and Analysis

For each line, larval shell length was determined from a random sample of 40 larvae taken at 2-d intervals from day 2 to day 8. These data were analyzed by restricted maximum likelihood techniques using a model of the general form

$$Y_{ij} = u + G_i + e_{ij}$$

where u is the population mean common to all observations, G_i is the fixed effect due to the ith mating ($i = 1, \ldots, 6$), and e_{ij} is a residual effect peculiar to the jth observation on the ith mating.

At 3.5 mo of age, shell length was taken on a random

TABLE 1. Mean shell length (μm) and standard error (in parentheses) of a sample of 40 larvae derived from the Bouctouche (B), Miramichi (M), Shemogue (S), Miscou (Msc), St-Simon (Sm), and Richibouctо (R) populations and their crosses.

Age (d)	Parental population	(μm)	Cross	(μm)	Heterosis[a] (%)
2	B	63.3(0.53)	B × M	71.0(0.67)	15.4
	M	59.7(0.56)	S × M	67.9(0.74)	10.9
	S	62.7(0.69)	B × S	56.0(0.41)	−11.1
	Msc	70.2(0.43)	Msc × Sim	73.0(0.51)	3.6
	Sim	70.7(0.41)	R × Sim	72.2(0.58)	0.8
	R	72.6(0.39)	R × Msc	—	—
4	B	95.6(1.04)	B × M	100.5(2.04)	9.0
	M	88.7(0.99)	M × S	113.4(2.02)	23.5
	S	95.0(1.03)	B × S	81.0(0.47)	−15.0
	Msc	90.2(1.35)	Msc × Sim	99.1(1.49)	9.9
	Sim	90.2(1.49)	R × Sim	82.5(1.39)	−9.1
	R	91.4(1.28)	R × Msc	—	—
6	B	148.6(3.28)	B × M	121.0(1.90)	−14.4
	M	134.2(2.66)	S × M	158.7(2.47)	25.3
	S	123.0(2.30)	B × S	103.0(1.38)	−24.2
	Msc	108.7(2.04)	Msc × Sim	124.9(2.48)	14.0
	Sim	110.5(2.33)	R × Sim	108.0(2.67)	−1.5
	R	108.7(1.90)	R × Msc	—	—
8	B	212.0(4.30)	B × M	137.9(2.00)	−32.0
	M	193.6(3.90)	S × M	197.7(3.50)	8.6
	S	170.5(5.20)	B × S	123.0(2.00)	−35.7
	Msc	145.7(3.70)	Msc × Sim	158.6(5.20)	4.6
	Sim	157.8(4.34)	R × Sim	133.0(4.40)	−9.0
	R	134.6(3.48)	R × Msc	—	—

[a]Mean deviation of the crosses from their parental populations expressed as a percentage of the parental population mean.

sample of each cross directly on the scallop shells. In May 1978, individual records were maintained and estimates of shell length and survival were recorded in the fall of the next 3 yr. A combined meat and shell weight was obtained at the termination of the experiment. Analysis of these data was made using the mixed model

$$Y_{ijkl} = u + G_i + L_j + GL_{ij} + S_k + e_{ijkl}$$

where u is the population mean common to all observations, G_i is a fixed effect due to the ith mating ($i = 1, \ldots, 6$), L_j is a fixed effect due to the jth location ($j = 1, \ldots, 2$), GL_{ij} is a fixed effect of the jth location and the ith mating, S_k is a random effect due to the kth setting date ($k = 1, \ldots, 4$), and e_{ijkl} is a residual effect peculiar to the lth observation of the kth setting, jth location, and ith mating.

Restricted maximum likelihood estimates were obtained by means of Biomedical Programs P-series (Jennrich and Sampson 1979). Growth patterns were evaluated in terms of absolute shell length, and weight at 40 mo. The survivorship curves were statistically compared based on a Lee and Desu test (1972).

Results

All crosses but B × S had a larval shell length at day 2 greater than that of the unweighted average of appropriate mean parental populations (Table 1). Generally speaking, the relatively superior performance of the crosses (three of which exceeded the better parental population at day 2) was not maintained. At day 8, none of the crosses exceeded the best parental population and only one (S × M, t-test at 0.05) showed a mean larval shell length greater than the mean parental population. Substantial differences in larval shell length at day 8 did not appear to influence the time to first appearance of metamorphosed larvae (about 12 d from fertilization). Attempts to characterize larval survival were found to be unreliable and the data are not reported.

The three populations and their crosses that survived the 1977−78 winter were followed for 3 yr. Differences between locations (Table 2) were much greater than differences among groups within locations (Table 3) for both length and weight measurements. The oysters growing at Richibouctо would reach marketable size 1 yr earlier than those at Shippagan. The difference between locations was especially marked from 11 to 16 mo where the average length change was 16.2 mm at Shippagan but 29.5 mm at Richibouctо (Table 2). The relative growth rate of the genetic groups was site dependent, and significant genotype × location interactions were present for both length and weight characters (Tables 3, 4, 5). For example, the Bouctouche parental population ranked first at Richibouctо, but fourth at Shippagan. The analysis of variance on weight at 40 mo (Table 5) illustrates the relative importance of genetic groups, locations, and their interaction and is general for other traits. Although there was only one

TABLE 2. Restricted maximum likelihood estimates (AVE) with two standard errors of juvenile to adult shell length at different times and weight at 40 mo at two locations.

Trait	Age (mo)	Shippagan[a] AVE	Shippagan[a] 2SE	Richiboucto[a] AVE	Richiboucto[a] 2SE	Locations combined[a] AVE	Locations combined[a] 2SE
Length (mm)	3.5	7.8	0.01	8.5	0.01	8.1	0.00
	11.0	10.6	0.02	13.3	0.02	11.9	0.01
	15.5	26.8	0.05	42.8	0.05	34.8	0.03
	30.0	42.1	0.08	56.8	0.09	49.2	0.05
	40.0	57.7	0.12	66.8	0.14	62.2	0.08
Weight (g)	40.0	33.3	0.17	48.2	0.20	40.8	0.11

[a]Mixed model with environments as fixed variables and group, group × locations as random variables.

TABLE 3. Restricted maximum likelihood estimates (AVE) with two standard errors (in parentheses) of juvenile and adult shell length (in mm) at 5, 11, 16, 30, and 40 mo for the pure population matings and in crosses at two locations.

Age (mo)		Shippagan M AVE(2SE)	Shippagan B AVE(2SE)	Shippagan S AVE(2SE)	Richiboucto M AVE(2SE)	Richiboucto B AVE(2SE)	Richiboucto S AVE(2SE)
5	M	7.5(0.0)	7.7(0.0)	7.6(0.0)	8.3(0.0)	8.7(0.0)	8.2(0.0)
	B		8.2(0.1)	7.8(0.0)		8.7(0.0)	7.8(0.1)
	S			8.1(0.0)			8.6(0.0)
11	M	10.7(0.1)	10.2(0.0)	10.1(0.1)	12.9(0.1)	13.6(0.0)	12.9(0.0)
	B		10.8(0.1)	10.7(0.1)		13.0(0.1)	11.9(0.1)
	S			11.0(0.0)			14.3(0.0)
16	M	27.5(0.1)	27.6(0.1)	27.2(0.1)	38.6(0.1)	45.0(0.1)	41.8(0.1)
	B		25.7(0.1)	25.7(0.1)		43.7(0.1)	41.4(0.1)
	S			27.2(0.1)			45.3(0.3)
30	M	39.9(0.2)	42.4(0.2)	43.8(0.2)	50.7(0.3)	58.1(0.2)	55.9(0.2)
	B		40.6(0.2)	40.3(0.2)		58.1(0.2)	55.2(0.2)
	S			45.1(0.2)			59.1(0.2)
40	M	54.7(0.3)	58.7(0.2)	60.3(0.3)	56.4(0.4)	70.0(0.2)	69.0(0.3)
	B		56.8(0.3)	56.1(0.2)		69.7(0.3)	66.2(0.6)
	S			60.1(0.2)			68.6(0.3)

TABLE 4. Restricted maximum likelihood estimates (AVE) of weight (g) at 40 mo with two standard errors. HET is the mean deviation of the crosses from the unweighted average of the parental populations as a percentage of the parental populations.

Cross	Shippagan AVE(2SE)	Shippagan HET %	Richiboucto AVE(2SE)	Richiboucto HET %	Locations combined AVE(2SE)	Locations combined HET %
M	29.4(0.4)		33.7(0.5)		31.7(0.3)	
B	33.5(0.3)		53.9(0.4)		43.4(0.2)	
S	34.6(0.3)		50.3(0.3)		42.6(0.3)	
M × B	34.5(0.3)	9.9	53.3(0.3)	21.0	42.3(0.2)	10.0
M × S	35.8(0.3)	11.9	48.0(0.3)	14.3	41.3(0.2)	11.2
B × S	32.1(0.3)	−5.6	50.2(0.7)	−3.6	41.1(0.3)	−4.4

degree of freedom for the location effect, its contribution to the total variance was by far the most substantial. The interaction of genetic group and location contributed significantly to the variation also and is comparable with that of the genetic groups.

There were substantial differences between crosses. Both

TABLE 5. Analysis of variance table and estimates of variance components of weight at 40 mo at two locations (**$P < 0.01$).

Source	df	Mean square	F	Variance component
Groups (G)	4	3076.3**	15.4	12.2
Locations (L)	1	55465.0**	277.3	108.6
G × L	5	1280.7**	6.4	14.3
Error	1110	200.0		200.0

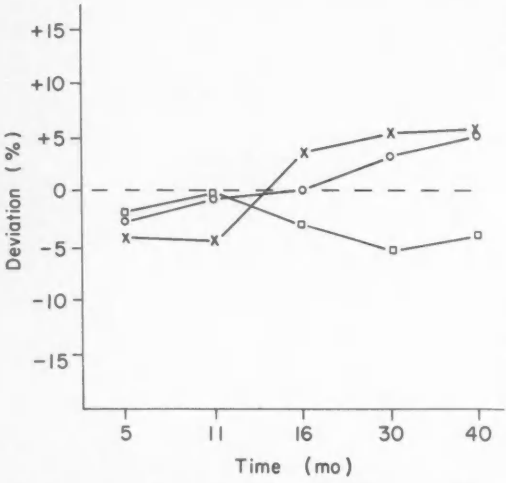

FIG. 1. Mean shell length of crosses minus the unweighted average of the appropriate parental population means as a percent departure from this latter in the Shippagan environment. The maximum 2SE about each point is 0.05%. ×, BM; ○, MS; □, BS.

positive and negative mean deviation of crosses from the mean parental population were observed (Fig. 1 and 2). The B × S cross showed consistent negative values for both shell length and weight. The magnitude of heterosis was greater at Richibouctо, but the ranking at 40 mo was the same in both environments.

At the termination of the experiment no significant difference in survival between locations was found based on a Wilcoxon sign-ranked test ($P > 0.05$) (Table 6). However, the survival of the crosses exceeded that of pure matings (Fig. 3). The survivorship curves were derived from the pooled data of the three within- and the between-population crosses, respectively. Based on a Lee and Desu (1972) test, the difference between the survivorship curves was highly significant ($P = 0.004$).

Discussion

Substantial population differences were observed for the following traits: larval shell length at different stages, juvenile and adult shell length, weight, and survival. With regard to the localities studied, an initial gain of 35% in weight at 40 mo could be achieved by choosing the Bouctouche rather

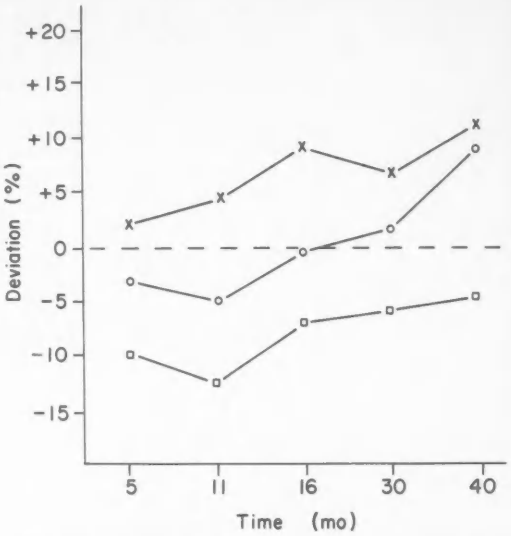

FIG. 2. Mean shell length of crosses minus the unweighted average of the appropriate parental population means as a percent departure from the latter in the Richibouctо environment. The maximum 2SE about each point is 0.05%. ×, BM; ○, MS; □, BS.

TABLE 6. Percent survival for the parental populations and crosses expressed as the proportion surviving at the termination of the experiment from spring-labeled 1978 oysters.

Cross	Shippagan (%)	Richibouctо (%)	Locations combined (%)
M	56.1	45.2	50.7
B	55.4	55.5	55.4
S	56.9	55.2	56.1
BM	63.8	63.0	63.4
MS	51.1	51.3	51.2
BS	67.8	67.2	67.4
Total	58.5	56.2	

than the Miramichi population. Such potential gain can be compared with a 23–25% increase in weight at 24 mo in *Ostrea edulis* for one generation of selection (Newkirk 1983).

The presence of nonadditive gene effects as shown by the heterosis in larval characters is unquestionably substantial, and although biologically interesting, it cannot be interpreted meaningfully with this data set. The pooling of the reciprocal crosses does not allow the estimation of maternal effects on larval shell length at day 2; however, a subsequent experiment (in preparation) will provide a fuller analysis of larval growth rate and survival. Newkirk (1978) reported the mean larval survival of four population crosses to be very close to the mean of the pure matings from day 2 to day 14 although one hybrid cross showed overdominance. He also observed nonadditive gene effects in the trait larval surface area (highly correlated with length). Initial larval shell length could,

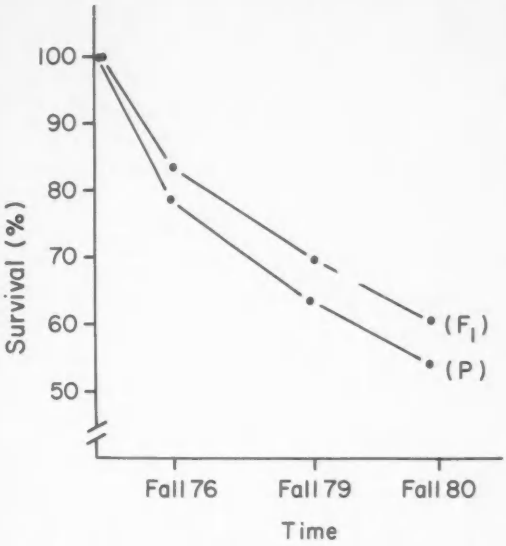

FIG. 3. Survivorship of pooled parental populations (P) and pooled crosses (F_1) after spring 1978 identification.

however, be correlated with such traits as larval survival and percent metamorphosis, and this should be investigated.

For the juvenile and adult characters our study suggests the following.

1) In growth the locality main effect is clearly significant. Its contribution to the total variance is greater than that of genetic groups, although greater gains are still achieved with the choice of the population appropriate for a specific location. There exist significant group × location interactions so that a genetic group performing well in one location might not do so well in a different one, relative to the other groups (Table 3).

2) The locality contribution for juvenile to adult survival is nonsignificant; however, the genotypic effect is expressed in the higher survival of crosses as compared with pure population mating. Similar trends in growth and survival characters have been recorded in *Mytilus edulis* (Dickie et al., in preparation).

3) Significant deviations of crosses from the mean parental population were observed in juvenile to adult characters. These deviations are heterosis, defined as the deviation (+ or −) of the crosses from the mean of the parental populations (Falconer 1980; Sheridan 1980). It should be pointed out that the performance of the crosses was measured as a departure from noninbred lines, and any gain is a real increase as opposed to the mere recovery from the accumulated effects of inbreeding depression. The crosses demonstrated generally a higher survival and their weight was, in three instances, as good as the better parental populations. These results imply the presence of nonadditive gene effects for most of the traits but do not imply that crossbreeding is warranted. The negative deviation of the between-population cross, B × S, from the mean parental population is substantial: this could be caused by some genetic mechanisms, maternal effect, or genetic sampling problems but no explanation can be proposed at this stage.

4) The level of confidence in ranking the matings at any location depends on the relation between year to year variability and the length of the evaluation period. Although our results are based on 40 mo of performance data, all but one of the rankings could have been ascertained at 12 mo (Table 3). The between-year within-location component must be relatively small; hence, it is concluded that 2 yr of performance data should generally be sufficient to estimate reliable rankings.

Previous experiments (Newkirk 1980; Haley and Newkirk 1977) have described a large additive genetic component, suggesting that mass selection is appropriate for improving growth traits. However, from the present experiment, it appears there is substantial nonadditive variability that should be exploited as well. Edwards and Gjedrem's (1979) data on the percent survival to swim-up of brown trout interstrain crosses indicated that three of four crosses are expected to have a higher average survival than the mean of the two parental strains, being indicative of considerable heterosis. Moav et al. (1975) found little or no additive variability in growth traits of the European carp. However, crossbreeding between the European carp and the Chinese carp was successful and showed significant gain; 20% increase in weight at 1 yr of age was achieved. An increase of 10% per generation time produced by artificial selection can indeed be regarded as a considerable improvement in performance. Values ranging between 2 and 5% are actually of more common appearance in the animal breeding literature. The use of population combinations would certainly be judged as appropriate based on the data gathered in this study. The mean interpopulation performance averaged over the two environments at the end of the experiment was 5.9% greater than the pure matings in surface area, 5.6% higher in weight per individual, and had an increased survival of 12.4% as well. This analysis therefore supports the view that oysters conform to other nonmarine models.

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Morphological Study of Sieve Efficiencies and Mandibular Surfaces in the Antarctic Krill, *Euphausia superba*

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MCCLATCHIE, S., AND C. M. BOYD. 1983. Morphological study of sieve efficiencies and mandibular surfaces in the Antarctic krill, *Euphausia superba*. Can. J. Fish. Aquat. Sci. 40: 955–967.

The filtering basket of *Euphausia superba* is a complex comb filter with a wide range of mesh intervals. Intersetal distances range from approximately 15–95 μm between primary setae to 4–18 μm between secondary setae (setules). Microsetules with spacing of 1–2 μm thicken boundary layers surrounding secondary setae. Reynolds numbers for setules and microsetules, ranging from 0.006 to 0.95, limit the feeding modes available to *E. superba* for suspension feeding. Relative efficiency of particle capture, estimated from intersetule mesh size and grazing experiments with small phytoplankton (<30 μm), show an asymptotic efficiency for particles 12–28 μm. Setule frequency distribution conservatively characterizes particle size selection for these small particles. The fine structure of the mandibular pars molaris varies between krill species and shows specialized surfaces that can split diatom chains, cut or fracture hard tests, and grind particles smaller than 10 μm.

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Le panier filtreur d'*Euphausia superba* est un dispositif en peigne complexe, avec gamme étendue d'intervalles de maille. Les distances intersétales sont comprises entre les extrêmes d'environ 15–95 μm d'une soie primaire à l'autre et de 4–18 μm entre soies secondaires (sétules). Des microsétules espacés de 1–2 μm épaississent les couches frontières entourant les soies secondaires. Les nombres de Reynolds touchant les sétules et les microsétules, variant de 0,006 à 0,95, limitent les modes d'alimentation dont dispose *E. superba* en vue de la capture de proies en suspension. L'efficacité relative de capture des particules, estimée à partir de la grandeur des mailles intersétules et d'expériences de broutage avec du phytoplancton de petite taille (<30 μm) montrent une efficacité asymptotique à l'endroit de particules de 12–28 μm. La distribution des fréquences des sétules caractérise de manière conservatrice le choix de la taille des particules dans les cas où ces dernières sont petites. La microstructure de la pars molaris mandibulaire varie d'une espèce de krill à l'autre et montre des surfaces spécialisées capables de briser des chaînes de diatomées, de couper ou fracturer des tests durs et de broyer des particules de taille inférieure à 10 μm.

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THERE has been increasing interest in fishing krill, *Euphausia superba*, for use in protein meal, animal feed, oil, dietary supplements in aquaculture, and for human consumption. Krill is the pivotal animal in Antarctic food webs, so that energy transfer to higher trophic levels necessarily depends upon their feeding efficiency and the trophic levels that they occupy. However, feeding data for krill is still relatively scanty, particularly concerning aspects of selective feeding. Quantitative data on functional feeding responses in relation to particle size and concentration are required to estimate production using an energy budget approach. Such information is basic to the development of management regimes necessary to regulate the fishery for krill in the Antarctic.

Our objective was to present data, based on morphology and feeding experiments, showing that krill feed with high efficiency on nanoplankton (2–20 μm in diameter). Although the finely barbed feeding appendages of *E. superba* are capable of retaining phytoplankton as small as 10 μm (Barkley 1940; Nemoto 1967), qualitative gut content studies, which revealed a high proportion of small phytoplankton in krill stomachs (Barkley 1940; Hustedt 1958), give a biased impression of krill selectivity (Pavlov 1971). Studies of the feeding efficiency of krill on small particles have been nonexistent until recently (Meyer 1981; Boyd et al. 1983; Morris 1983). Nanoplankton constitute 70% of the phytoplankton biomass in some oceanic Antarctic waters (El Sayed and Turner 1974; Fay 1973) and are believed to be responsible for 90% of the primary production (Von Brockel 1981). The flagellates that dominate this size class lack refractory structures that could be identified from the gut contents of grazing

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krill. *Euphausia superba* has well-developed clusters of spines on the lateral plates of the stomach that form a gastric mill (Nemoto 1967). The effect of this digestive mechanism prevents identification of any but the most robust food items by gut content analysis. However, it is possible to take a morphological approach and to infer the retention efficiency for small particles from the structure of the feeding appendages of *E. superba*.

Further information on diet can be deduced from the fine structure of the mandibles. Although the mouthparts of adult krill have been described many times (Mauchline 1967, 1980; Nemoto 1967, 1977; Barkley 1940; Lomakina 1973), there are no scanning electron microscope (SEM) studies of the mandibles, so their fine structure has been missed by earlier studies. Grice and Lawson (1971) demonstrated the usefulness of SEM for description of copepod mandibles. The depth of field provided by SEM is particularly suited to examination of the thick pars molaris of euphausiid mandibles.

The morphological approach to particle size selection has principally been applied to copepods. Passive mechanical sieving of particles was proposed by Nival and Nival (1973, 1976, 1979) for *Acartia* and by Boyd (1976) as a general principle. This approach was supported with some reservations by Frost (1977) and Runge (1980) working on *Calanus pacificus* and by Vanderploeg (1981) for *Diaptomus*. Vanderploeg and Ondricek-Fallscheer (1982), however, found the setule model inadequate to explain selectivity by *Diaptomus* at larger particle sizes. Artiges et al. (1978) constructed a mechanical filtering model for the filtering baskets of *Meganyctiphanes norvegica* and *Euphausia krohnii*. The work of U. Kils (Institut für Meereskunde, Dusternbrooker Weg 20, D2300 Kiel, Federal Republic of Germany, personal communication) was the only other attempt to apply this principle to euphausiids.

Perhaps the most significant argument against mechanical selection comes from cinematographic studies and consideration of the fluid mechanics of filters under viscous conditions. At low Reynolds numbers, boundary layers around setules may be thick enough to prevent movement of water through the filtering meshes so that the second maxillae of calanoid copepods behave more like paddles than like stationary sieves (Koehl and Strickler 1981; Alcaraz et al. 1981; Paffenhofer et al. 1981). Particles follow streamlines and can be moved towards the mouthparts without touching the appendages. Calculations of the filter area required to sieve volumes swept clear of particles by calanoids show the filter to be much too small for the task (Koehl and Strickler 1981). As we will show, this is not the case in *E. superba*. Furthermore, even in copepods, setule spacing is important for retaining small particles (Strickler 1982) and may determine the minimum size of particle that can be retained (Bartram 1980). Setule length, spacing, and stiffness should also affect which particles are retained as water is compressed within the closing maxillae when particles contact the feeding appendages (Koehl and Strickler 1981).

Three different modes of suspension feeding have been proposed for krill, apart from raptorial feeding. These are stationary filtration (Berkes 1975; Kils 1979; Ponomareva 1963), plankton net filtration (Barkley 1940; Kils 1979; Berkes 1975), and flailing of the limbs constituting the filtering basket (Boyd et al. 1983; Antezana et al. 1982; Berkes 1975). Consideration of viscous flow across the filtering basket places severe constraints on the operation of these mechanisms.

Materials and Methods

In addition to *E. superba*, SEM of mandibles and pereiopods was carried out on three euphausiid species common in Nova Scotian shelf and slope waters (*M. norvegica*, *Thysanoessa longicaudata*, and *E. krohnii*). Formalin-preserved specimens were prepared for SEM by rinsing with stepwise dilution to distilled water, followed by gradual replacement with ethanol. Specimens were critical point dried with CO_2, mounted on double stick tape, sputter coated with gold–palladium (200 nm), and then examined in a JEOL-35 or a NANOLAB 2000 SEM.

Observations of the filtering basket were made on 12 adult *E. superba*, 23–48 mm long (tip of rostrum to posterior margin of telson). Mesh intervals of the filtering basket were measured from water mounts of pereiopods. Distances between the inner margins of the bases of the primary setae were measured (at 125× magnification) between every fifth seta and its neighbor along the ischium and merus segments of the leg. The narrower intersetule distances, taken as the interval between the inner bases of adjacent secondary setae, were measured (at 400×) at even intervals along the primary setae. Measurements were taken from two krill (47.6 and 30.4 mm) to determine whether mesh sizes differed between the six legs of the filtering basket. Pairwise comparison with the sixth pereiopod (*t*-test, assuming unequal variances, Sokal and Rohlf 1981) revealed no significant differences between the appendages ($P > 0.05$). Mean primary and secondary mesh sizes from the sixth pereiopod on all krill were plotted against krill length to determine the relation between krill size and mesh intervals. Frequency distributions of primary and secondary mesh sizes from ischium and merus were pooled to produce cumulative distributions. Microsetule intervals were estimated from SEM photographs. Thirty-five microsetule intervals were measured from three different areas of the appendage, photographed at 3000× magnification.

The total area of the filtering basket was measured as twice the sum of the filter on each of the six legs constituting the basket, using approximation to geometric shapes. An attempt to measure the area covered by secondary setae alone using camera lucida was hampered by the V-shaped projection of setules out of the plane of focus and their probable deformation from their position in vivo.

Grazing experiments were run using natural phytoplankton assemblages and individual krill, rotated in bottles on a plankton wheel. Particle counts were analysed with a TA II Coulter counter. Cells in the size range discussed here were mainly small centric and ellipsoidal pennate diatoms. Experiments were run at Arktowskii Station by C. M. Boyd. Methodological details are published elsewhere (Boyd et al. 1983).

Results

The generalized morphology of the pars molaris in *E. superba*, *M. norvegica*, *E. krohnii*, and *T. longicaudata*

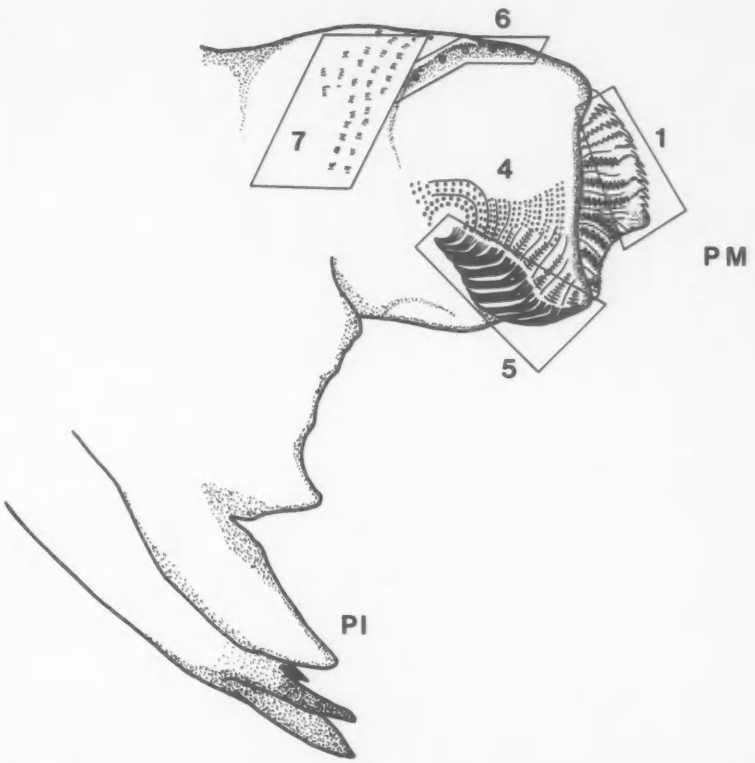

FIG. 1. Generalized fine structure of euphausiid pars molaris as exemplified by left mandible of *M. norvegica*. PM, pars molaris; PI, pars incisiva. Regions: 1, serrated marginal teeth; transitional regions 2 and 3 lie on either side of median ridge; 4, platelike grinding region; 5, finely divided marginals; 6, marginal pores; 7, sencillae.

consists of five regions and two transition zones (Fig. 1). Marginal teeth are more finely divided at their tips on the proximal side of the molar (region 5) than on the distal side where they are more serrated or spinelike (region 1). Marginal teeth grade into two distinct transitional zones (regions 2 and 3) as the central dividing ridge of the molar is approached. Much of the proximal side of the ridge is a platelike area consisting of rows of depressions (region 4). The basal margin of the molar has regularly spaced pores (region 6). The supporting structure for the grinding surface of the molar is covered by rows of grouped minute setae, assumed to be sencillae (region 7). Detailed structure of the regions is shown in Fig. 2 and 3.

The generalized regions show interspecific differences. Region 5 is dominated by spines in *E. superba* (Fig. 2C, 2D), but is finger-like in *T. longicaudata*, and progressively more brush-like in *M. norvegica* (Fig. 3C) and *E. krohnii*. Region 1 is also sharply spinose in *E. superba* (Fig. 2C, 2D), becoming more bluntly serrated in *M. norvegica* and *T. longicaudata*. The platelike region 4 is best developed in *E. superba* (Fig. 2), becoming progressively less extensive in area in *M. norvegica*, *E. krohnii*, and *T. longicaudata*. Marginal pores (region 6, Fig. 2D) were present in all four species, as were groups of sencillae (region 7, Fig. 3B), which may possibly be chemoreceptors. Although mandibular chemoreceptors have been found on copepods (Sullivan et al. 1975; Ong 1969), they have not been reported from euphausiids.

As reported previously for the pars incisiva (Mauchline 1980; Lomakina 1973), the pars molaris is assymmetrical. The molars are positioned dorsally to the incisor blades. The convex ridge of the left molar fits into the broad concavity of the right molar. The right molar bears a notch in the posterior margin (Fig. 3A), which receives a protuberance on the left molar, thereby aligning the molar surfaces. The anterior margin of the right molar fits a groove in the same margin of the left molar, aiding the alignment. This arrangement brings the platelike surfaces (region 4) into close contact over much of their area, suggesting the capability for very efficient crushing and grinding.

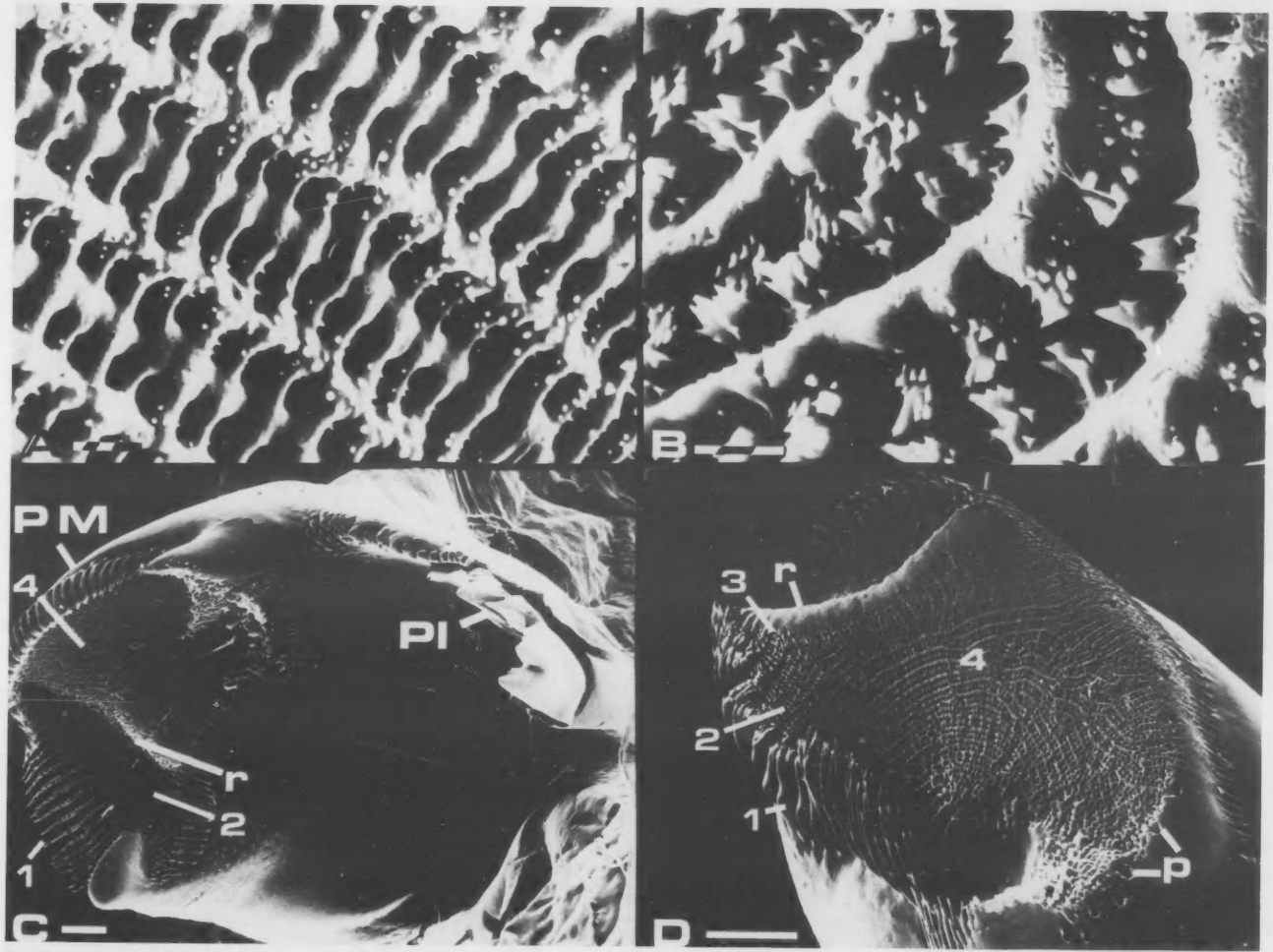

FIG. 2. (A) Close-up of region 4 on *E. superba* pars molaris; bar = 5 μm. (B) Close-up of transitional region 3 showing cusps; bar = 5 μm. (C) Mandible of *E. superba* showing the pars molaris (PM), pars incisiva (PI), and the median ridge of the molar (r). Regions 1–4 represent different cutting and grinding surfaces (see Fig. 1); bar = 100 μm. (D) Lateral view of the pars molaris. p, marginal pores; bar = 100 μm.

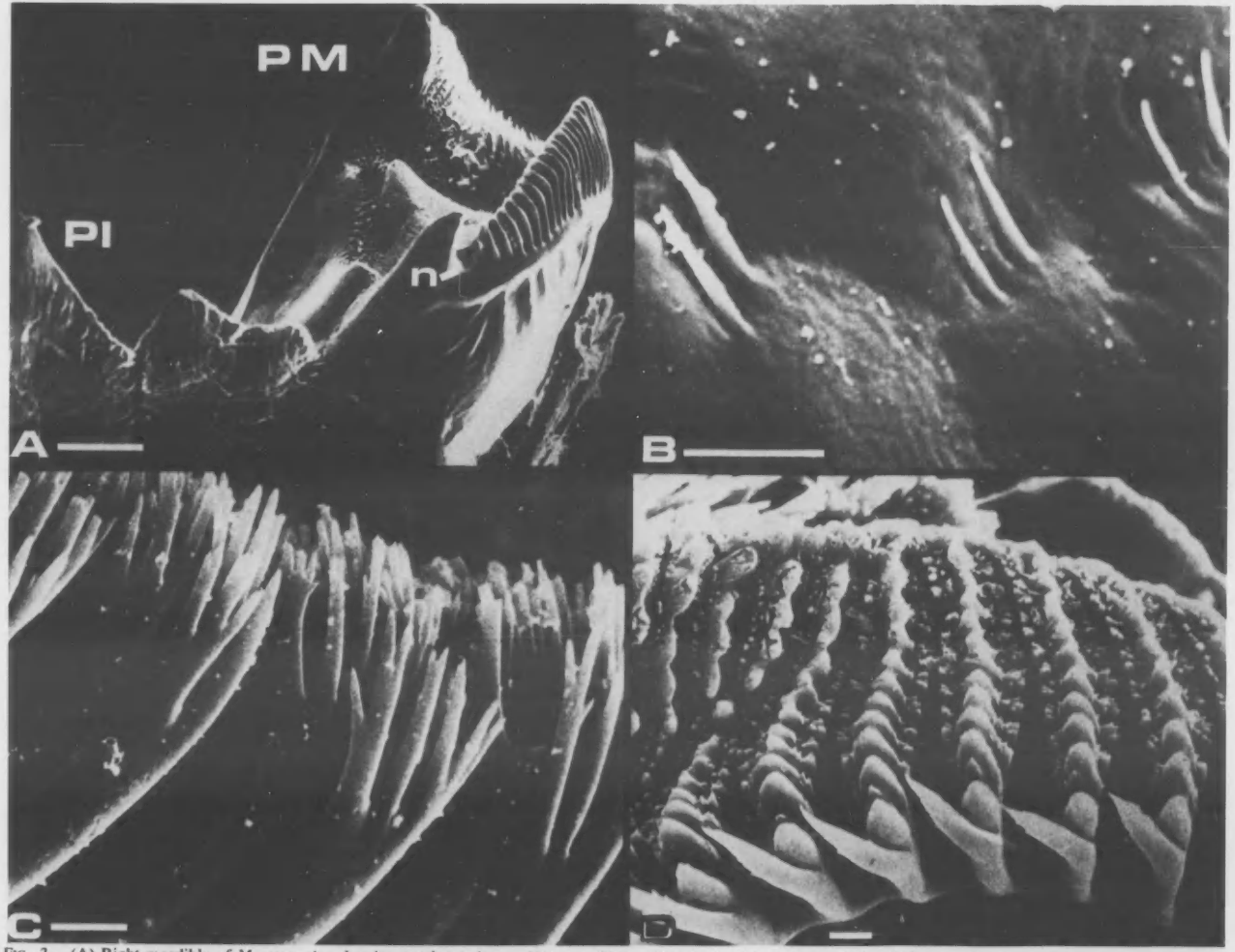

FIG. 3. (A) Right mandible of *M. norvegica* showing notch (n); bar = 100 μm. (B) Sencillae (region 7) on pars molaris of *M. norvegica*; bar = 5 μm. (C) Finely divided marginal teeth (region 5) of *M. norvegica*; bar = 5 μm. (D) Marginal spines (region 1) on *E. krohnii* pars molaris; bar = 5 μm.

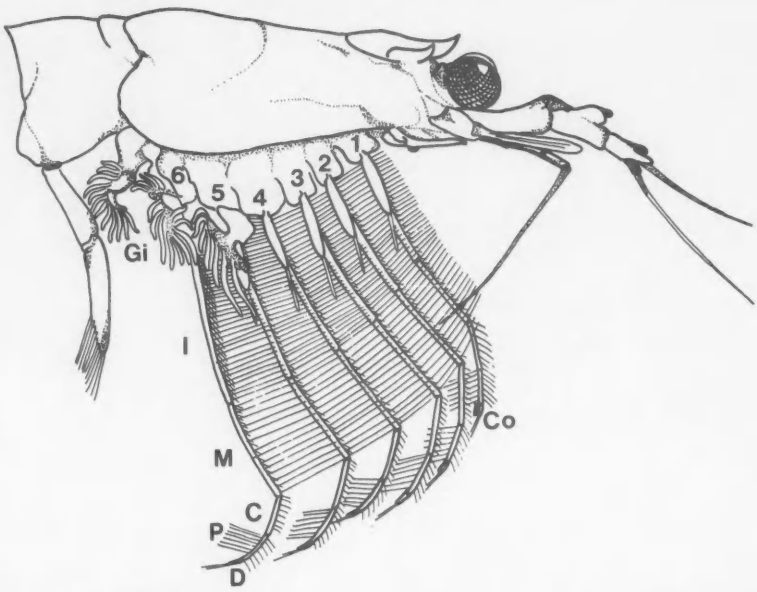

FIG. 4. Thoracic filtering basket of *E. superba*. Gills (Gi) on pereiopods 1−4 and left appendages removed. I, ischium; M, merus; C, carpus; P, propodus; D, dactylus; Co, comb setae.

The V-shaped filtering basket of *E. superba* formed by the six pereiopods (Fig. 4) is the principal food collection apparatus (Mauchline 1980; Barkley 1940). The basket is walled by anteriorly projecting primary setae (Fig. 5A, 5C), which overlap the ischium and merus of the next forward leg. Primary setae bear two rows of setules (secondary setae) arranged along their length in a wide-angled V-pattern (Fig. 5B, 5D). Primary and secondary setal intervals were normally distributed on the ischium and merus (Fig. 6). Mean intersetal intervals (±SD) for secondary setae were 6.5 ± 2.4 μm on the ischium and 9.3 ± 2.8 μm on the merus. Mesh intervals for primary setae were 34.5 ± 8.7 μm (ischium) and 58.2 ± 15.9 μm (merus). Although some separation of the distribution of setal intervals between proximal and distal segments was apparent, differences between the means were not significant (Mann-Whitney *U*-test: Wilcoxin paired comparison test, $P > 0.05$).

The variation in mesh intervals between secondary setae was greater than 5−7 μm (Barkley 1940) or 4−5 μm (Dzik and Jazdzewski 1978) although the modal mesh sizes were 5 μm for the ischium and 7 μm for the merus. SEM examination of the filtering basket revealed microsetules (tertiary setae) arranged in a single row along the secondary setae (Fig. 5B). Microsetules are 0.5−1.0 μm long, spaced at 1- to 2-μm intervals. Microsetules also occur in *Meganyctiphanes norvegica* and *E. krohnii* but they are much more widely spaced and not as prominent as in *E. superba* (Fig. 5D).

The area of the filtering basket increases with krill length ($A = 6.51L - 66.36$, $r^2 = 0.83$) (Fig. 7). Filter areas are 26−100 mm^2 for a 20-cm krill compared with 220−295 mm^2 for a 50-mm krill (95% confidence intervals). The cumulative frequency distribution for intersetule distances is given in Fig. 8. Setules do not form a closed mesh over much of the filter, so that an approximate correction for areas where the setules appear as combs rather than interlocking meshes can be included. This was estimated as the proportion of the total filter covered by setules (0.8), but the correction cannot be applied rigorously because the setae do not lie in the horizontal plane, and so the area is likely to differ in vivo and beneath a coverslip.

The mean mesh interval between primary setae varies with krill length according to the relationship $M = 1.6L - 4.3$, $r^2 = 0.81$) (Fig. 9). Primary setae mesh sizes are 19−36 μm for a 20-mm krill compared with 68−83 μm for a 50-mm krill (95% confidence intervals). Secondary setae meshes do not, however, vary consistently with krill size. Mean intersetule intervals vary by only 4 μm between krill ranging from 20 to 50 mm long. The cumulative distribution for primary setae mesh intervals must be adjusted for krill of different sizes, using the regression of mean primary setae intervals on krill length. Mesh intervals are normally distributed, so that for krill of a given size, the predicted mean mesh size corresponds to the mode of the frequency distribution. The mean mesh size will correspond to the 50% point of the cumulative frequency distribution, so that the curve can be shifted to right or left depending on the size of the krill (Fig. 10).

Relative efficiency of capture for particles smaller than 30 μm was calculated from Coulter counter data. Relative efficiencies were obtained by normalizing filtration rates in each size channel to the maximum clearance rate. The data

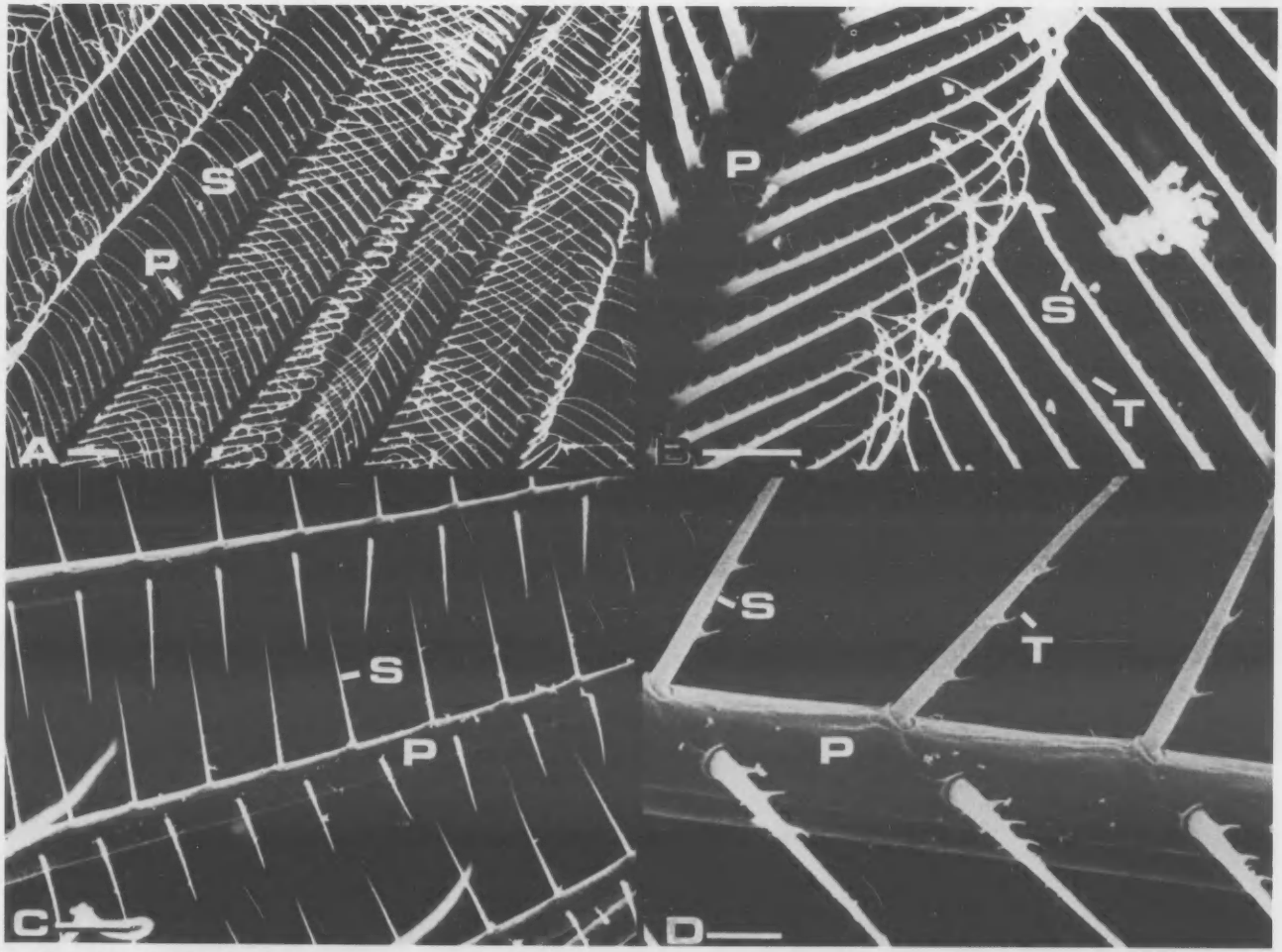

FIG. 5. (A) Setose mesh of the sixth pereiopod of the filtering basket of *E. superba*. P, primary setae; S, secondary setae. Bar = 25 μm. (B) Higher magnification of primary, secondary, and tertiary (T) setae; bar = 5 μm. (C) Setule mesh on ischium of *M. norvegica*; bar = 25 μm. (D) Close-up of same region showing tertiary setae; bar = 5 μm.

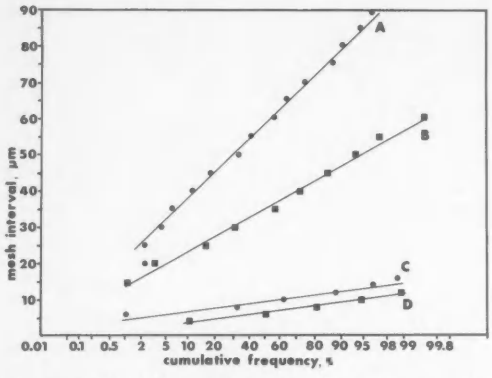

FIG. 6. Filtering basket mesh intervals for *E. superba* expressed as cumulative percent frequency on probability scale to show normal distribution. A, primary setae, merus; B, primary setae, ischium; C, secondary setae, merus; D, secondary setae, ischium.

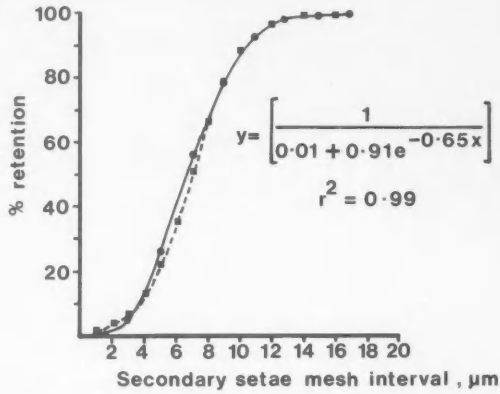

FIG. 8. Cumulative frequency distribution or predicted retention efficiency for secondary setae (setules). Broken line (solid squares) fitted by linearization and least squares method.

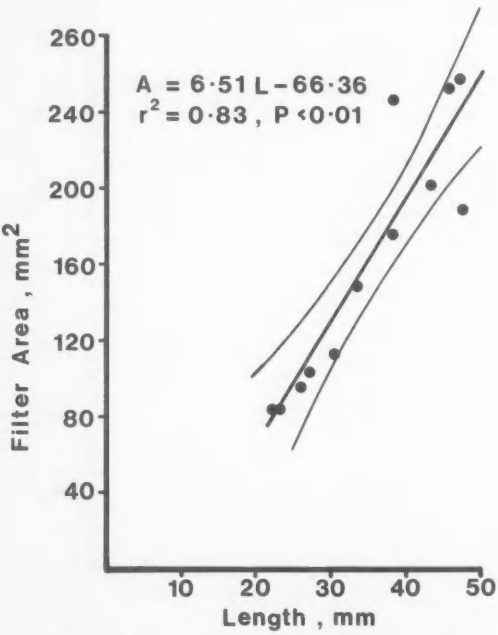

FIG. 7. Relationship between filtering basket area and krill size. Lines bracketing the least squares regression line are 95% confidence limits.

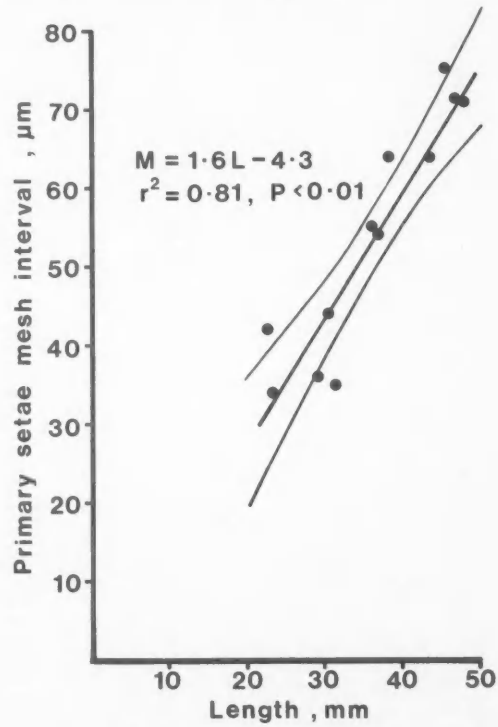

FIG. 9. Relationship between krill size and mean primary setae interval on ischium and merus. Lines bracketing least squares regression line are 95% confidence limits.

were fitted to two separate linear regressions with the inflection occurring at 10 µm (Fig. 11). Superimposing the fitted retention efficiency derived from the setule mesh distribution provides a remarkably close approximation to the experimental data for particles in the size range 7−30 µm. However, retention of particles sized 2.5−7 µm was higher in the experiments than predicted by the setule model. The mechanism of particle capture was direct interception, determined

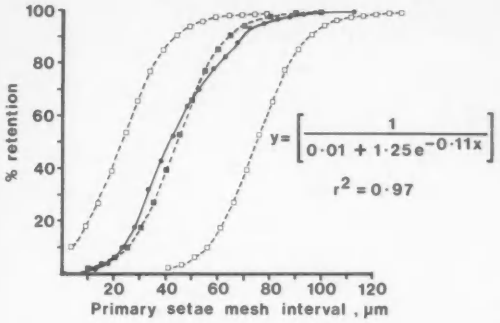

FIG. 10. Cumulative frequency or predicted retention efficiency for primary setae. Broken line (solid squares) fitted by linearization and least squares method. Predicted retention efficiencies for 17-mm krill (left) and 50-mm krill (right) obtained by translation of fitted curve using regression in Fig. 9.

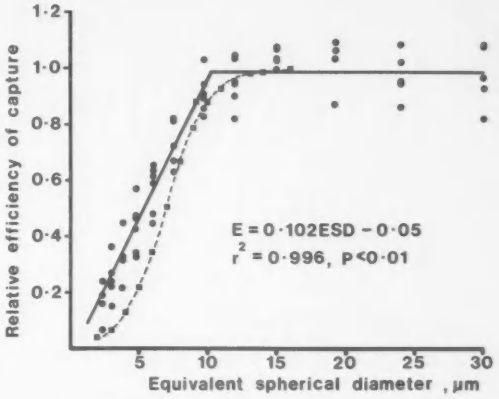

FIG. 11. Efficiency of particle capture as a function of particle size obtained from Coulter counter data. Relative efficiencies obtained by normalizing filtration rates in each size channel to maximum filtration rate. Least squares regression fitted using the mean of y values from individual krill, in the size range 2−10 µm, with the inflection point estimated by eye. Broken line represents predicted retention efficiency by setules (Fig. 8).

from Rubenstein and Koehl's (1977) dimensionless indices. This is in accord with most biological filters. Intensity of capture by direct interception increases at smaller pore sizes (Rubenstein and Koehl 1977), and boundary layers will exert a relatively greater effect, so that deviation from the setule model at very small particle sizes is not unexpected.

To ensure that krill can pass water through their filter, we examined the physical limitations of flow through the filtering basket. The dimensionless Reynolds number (Re) expresses the ratio of inertial to viscous forces in the fluid flow:

$$Re = UL\rho/\mu$$

where U is the flow velocity across the surface, L is the mesh size, ρ is the density, and μ the dynamic molecular viscosity of the fluid. At low Re (<1.0), viscous forces dominate inertial forces, and particles follow streamlines in laminar flow and cease movement when driving forces are removed. At high Re, flows are turbulent (Vogel 1981; Leyton 1975) and viscous forces are important only very near no-slip boundaries. The Re values were calculated for the modal mesh sizes (L) of primary, secondary, and tertiary setae using flow velocities of 4 and 25 $cm \cdot s^{-1}$, which Kils (1979) reported as the velocities between which the filtering basket would be fished like a net. At temperature = 0°C, salinity = 34.5‰, seawater density = 1.029×10^3 $kg \cdot m^{-3}$, and molecular viscosity = 1.89×10^{-3} $kg \cdot m^{-1} \cdot s^{-1}$, the thickness of the boundary layer (δ) around each seta of diameter d was calculated from (Ellington 1974)

$$\text{Order } (\delta^2/d^2\, Re) = 1$$

and compared with setal mesh intervals (Table 1).

Flow through the filtering basket should be dominated by viscous forces ($Re < 1.0$) even at the maximum forward swimming velocity (25 $cm \cdot s^{-1}$) for which the basket retains its shape. Despite the large size of *E. superba*, Re values for tertiary and secondary setae (0.03−0.95) lie within the range calculated by Koehl and Strickler (1981) for copepod filtering appendages (0.02−1.0). Boundary layer thickness around tertiary setae covers 60−100% of the interval between them. The tertiary setae mesh should, based on hydrodynamic considerations, effectively be impermeable to water flow and therefore will only serve to narrow the secondary setal intervals by increasing their boundary layer. At the velocities estimated by Kils (1979) for plankton fishing the basket, or at lower velocities, the inert boundary layers around the secondary setae are wide enough to impede flow through the setule meshes (Table 1). Filtration at these velocities appears to be hydrodynamically unlikely.

Discussion

The different molar surfaces of the mandible of *E. superba* represent a multifaceted grinding surface. The pars molaris is very effective in crushing hard-shelled food items such as diatoms, silicoflagellates, and foraminifera (Nemoto 1967). The differentiation of the grinding surfaces into very rugged cusped transitional areas and a broad platelike region indicates specialization for fracturing hard tests and for finer grinding of particles. Ridges on the latter surface are spaced at approximately 5-µm intervals, suggesting that particles smaller than 10 µm could be ground up effectively. Although the relatively large pars molaris of *E. superba* is characteristically that of a herbivorous euphausiid (Nemoto 1967) the marginal teeth are more spinelike than in the omnivore−carnivores *M. norvegica* and *T. longicaudata*. These spines resemble in outline the teeth of some pontellid copepods (Turner 1978) and may facilitate piercing of animal prey, functioning as an adjunct to the pars incisiva.

Barkley (1940) suggested that a feeding current entered the filtering basket as a result of the forward swimming motion of the krill. Kils (1979) reported that the filtering

TABLE 1. Estimated *Re* and boundary layer thickness surrounding tertiary and secondary setae of the filtering basket of *E. superba*. Velocities are maximum and minimum for plankton net filtration (Kils 1979).

Mesh type	Velocity ($cm \cdot s^{-1}$)	*Re*	Boundary layer thickness (μm)	One-half modal distance between setae (μm)
Tertiary setae	4	0.03	1	0.6
	25	0.16	<1	0.6
Secondary setae (ischium)	4	0.11	4	2.5
	25	0.68	2	2.5
Secondary setae (merus)	4	0.15	4	3.5
	25	0.95	2	3.5

TABLE 2. Estimated filter area required to sieve volumes swept clear of particles using a range of experimentally determined filtration rates from the literature. Velocities (V_0) are for stationary filtration and minimum velocity for plankton net filtration (Kils 1979), erring on the conservative side (see text for explanation). Filter areas calculated from regression $A = 6.51L - 66.36$.

Mean volume swept clear ($mL \cdot krill^{-1} \cdot h^{-1}$)	Krill length (mm)	Filter area (mm^2)	V_0 ($cm \cdot s^{-1}$)	Area required for sieving (mm^2)	% of filter area	Estimated V_0 assuming sieving ($cm \cdot s^{-1}$)
55.5[a]	17.8	49.5	0.6	2.6	5.3	0.03
			4.0	0.4	0.8	
947.1[a]	35.0	161.5	0.6	43.8	27.1	0.16
			4.0	6.6	4.1	
257.6[b]	33.1	149.1	0.6	11.9	8.0	0.48
			4.0	1.8	1.2	
135.0[c]	54.3	287.1	0.6	6.3	2.2	0.013
			4.0	0.9	0.3	
55.9[d]	55.9	297.5	0.6	9.7	3.3	0.02
			4.0	1.5	0.5	

[a]Morris 1983: flow through experiments.
[b]Morris 1983: static volume experiments.
[c]Kato et al. 1979.
[d]Antezana et al. 1982.

basket is forced open by swimming, thereafter maintaining a shape similar to that observed in krill holding the filtering basket open when hovering. Observations on *M. norvegica*, *Thysanoessa inermis*, and *T. raschii* showed that carmine particles accumulated in the food basket when the euphausiids were maintaining position by slow beating of their pleopods (Berkes 1975). Pleopod beat drives a flow in the anterior region of the body into which the filtering basket can be extended to capture particles. Velocities in this flow field are 0.3–0.9 $cm \cdot s^{-1}$ for *M. norvegica*, depending upon the strength of the pleopod beat (Kils 1979). If Reynolds numbers and boundary layer thickness are calculated using these velocities, flows are highly viscous around the setules ($Re = 0.006–0.03$) and the boundary layers prevent any flow through the setule meshes. Boundary layers extend 6–7 μm on either side of a setule, completely blocking flow through the secondary setae meshes (4–12.5 μm).

The *Re* calculations show that filtration cannot be accomplished by either fishing the feeding basket like a net or by holding it in the flow field generated by the pleopods. Boyd et al. (1983) and Hamner et al. (1983) described *E. superba* making periodic metachronal flailing motions with the pereiopods, capturing a parcel of water as the rapidly outflung legs are retrieved to the midline and adpressed to the body. In this feeding mode the filtering legs will presumably act as sieves when water is forced through the mesh as the filtering basket is collapsed. This can occur because as streamlines are compressed, velocity will increase, *Re* will also increase, and the width of the boundary layer around setules will decrease, so that water will be forced through the setule meshes. Particle retention by the filtering basket will then be determined by the distribution of mesh intervals in the filter. Antezana et al. (1982) described this feeding mechanism as repetitive, pulsatile extension and retraction of the thoracic legs occurring at a frequency of 2 $strokes \cdot s^{-1}$, the frequency depending upon food concentration. Berkes (1975) also mentioned that capture of large particles is by lateroventral movements of the thoracic limbs.

We propose, therefore, that to filter, the krill must use the flailing mode of feeding, which involves compression of water within the filtering basket. For krill to filter water using this mechanism, the area of the filtering basket must be great enough so that volumes swept clear of particles (determined experimentally) can pass through the filter. Using low estimates of velocity (4 and 0.6 $cm \cdot s^{-1}$, respectively, for plankton net and stationary filtration) and high and low filtration rates from the literature (55–947 $mL \cdot bug^{-1} \cdot h^{-1}$), we calculate that less than 27% of the filter area is required to filter the

volumes of water swept clear of particles (Table 2). This reflects a fundamental difference between the relatively small maxillary filter of copepods and the large thoracic filter of krill.

Retention efficiencies for euphausiids were predicted by Artiges et al. (1978) from the distribution of setule meshes on the filtering legs of *M. norvegica* and *E. krohnii*. Retention capacities were estimated to be 20−140 μm in *M. norvegica* and 20−120 μm in *E. krohnii*, both species having coarser setules than *E. superba*. Parsons et al. (1967) reported that 5 μm is the minimum particle size retained by *E. pacifica*. Intersetule spacings in this species are 7−12 μm (Nemoto 1967). Vanderploeg and Ondricek-Fallscheer (1982) demonstrated that setule mesh size distribution was inadequate to explain particle retention in *Diaptomus sicilis* because experimentally determined relative retention efficiencies declined at larger particle sizes in a manner not predicted by the asymptotic cumulative intersetule distances. Thus, while the morphological model of Nival and Nival appears to fit observed particle size selection in *Acartia*, it is not appropriate to *Diaptomus*. These authors attribute this difference to the different modes of suspension feeding in these species. *Diaptomus* holds its filter chamber stationary, and large particles can be swept off the meshes. *Acartia* uses a seining motion of the maxillary filter (Gauld 1966), which is similar to the flailing filtering mode of *E. superba*, except that krill use the thoracic legs instead of the second maxillae to capture particles.

Our knowledge of selective feeding by *E. superba* and other species of euphausiids is very limited. Barkley (1940) reported that small flat diatoms such as *Fragilaria* spp. were dominant in the stomachs of *E. superba*, suggesting that krill feed selectively on small diatoms. There is evidence for post-capture rejection of expanded or setose phytoplankton such as *Chaetoceros* spp., which are not taken into the mouth according to Nemoto (1967). Kawamura (1973) provided some correlative evidence that *E. superba* may avoid spiny diatoms. Krill concentrations appear to occupy areas where small diatoms, such as *Nitzchia curta*, are dominant, and to be absent from areas supporting abundant large setose diatoms such as *Corethron* and *Chaetoceros* spp. or the elongated *Rhizoselenia* spp. However, krill concentrations may occur in regions populated by small phytoplankton because the larger cells have been previously grazed down. Lists of phytoplankton species in krill stomachs by Barkley and Hart (compiled by Marr 1962) include six species of *Chaetoceros*, five species of *Rhizoselenia*, and the very large diatoms *Thalassiothrix antarctica*, *Corethron criophilum*, and the silicoflagellate *Distephanus speculum*. These forms were considered less important than the heavily silicified *Fragilariopsis antarctica* (*Nitzchia kerguelensis*), small (<40 μm) centric and *Fragilariopsis* section diatoms, and centric diatoms of 30−140 μm (*Actinocyclus*, *Asteromphalus*, *Biddulphia*, and *Coscinodiscus* spp.).

Inferences based on predicted passive retention of particles must be interpreted cautiously. Escapement of particles through the sieve will be more significant for distensible cells (e.g. flagellates) than for rigid diatoms (Boyd 1976). Escapement through plankton nets is due to both distortion of the meshes themselves and of the organisms forced against the meshes (Saville 1958). Boyd's (1976) estimate of escapement was based upon loss of zooplankton through silk meshes (Saville 1958) and does not appear to be adequate to characterize loss of phytoplankton cells. It is likely that no single value would serve for all types of phytoplankton cells, so that we have not attempted to parameterize escapement in our model. It is not known how the particles retained by the filtering basket are sorted at the mouthparts for size, morphology, or taste. Nonspherical particles introduce serious complications when determining the relevant dimensions for estimating particle size. Runge and Ohman (1982) reported that Nitex screens remove *Skeletonema costatum* and *Chaetoceros debile* approximately on the basis of their longest axial dimension, but the fusiform *Ceratium fusus* was removed according to its shorter axis because the cell orients lengthwise to flow streamlines. In contrast, passage of cylinder-shaped diatoms (*Thalassiosira angstii*, *T. weissflogii*) through the sieve was easily characterized by their cellular diameter.

Morphological evidence and grazing experiments indicate that filtering basket of *E. superba* will retain nanoplankton with high efficiency. Antarctic phytoplankton in this size range are mainly flagellates (5−10 μm in size), microflagellates (about 2 μm), and dinoflagellates (8−15 μm), with lesser numbers of pennate and centric diatoms (12−20 μm) (Von Brockel 1981). Krill stomachs often contain small centric diatoms such as *Thalassiosira gracilis* and *Coscinodiscus lentiginosus* (Hustedt 1958). The green amorphous material predominant in krill stomachs probably also consists partly of other less refractory nanoplankton, notably flagellates. Although the model we have presented is necessarily theoretical because of its morphological approach, the predicted retention efficiencies are supported by the high efficiency with which krill fed on nanoplankton in the grazing experiments.

Predictions based on mesh distribution provide a useful hypothesis against which the importance of behavioral selection can be tested. For particles larger than 30 μm, retention by primary setae should be of increasing importance. Mesh distributions predict >80% retention of particles larger than 40 μm for small krill (17 mm) or of particles >90 μm for large krill (50 mm). While the data of Meyer (1981) could be interpreted as supportive of this hypothesis, Morris (1983) obtained reduced retention efficiencies for particles larger than 25 μm with small to midsize krill (17.8−35 mm). Further data are required on the feeding efficiency of krill on large particles, but we believe that behavioral selection will dominate at larger particle sizes.

Krill exhibit versatile feeding behaviors in addition to suspension feeding, including carnivory, cannibalism, and detritus feeding (McWhinnie and Denys 1978, 1980; Boyd et al. 1983). Krill may also feed directly upon ice algae by scraping the underside of ice (Hamner et al. 1983). Raptorial feeding is certainly the likely means by which krill capture the large *Rhizoselenia*, *Corethron*, and *Chaetoceros* spp. found in their guts. However, the paucity of information on size-selective grazing in euphausiids justifies the morphological approach. We emphasize that our model provides a first approach to size selection in *E. superba* grazing on small particles.

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Bioeconomic Production Function in Fisheries: Theoretical and Empirical Analysis

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HANNESSON, R. 1983. Bioeconomic production function in fisheries: theoretical and empirical analysis. Can. J. Fish. Aquat. Sci. 40: 968–982.

The traditional "fishing effort" approach to fisheries economics implies the existence of a production function with fishing effort and fish abundance as independent variables. It is shown how the existence of bionomic equilibrium depends on the shape of this production function, as well as the demand and effort cost functions. The analysis is related to the recent discussion of collapses in fisheries occurring as a result of fish availability being inversely related to fish abundance. A Cobb–Douglas production function, with effort and fish biomass as independent variables, is estimated for the Lofoten fishery. This indicates that the availability coefficient increases as the fish stock is depleted. Finally, the fishing effort approach is integrated with neoclassical production analysis. Fishing effort is regarded as being produced by labor and capital, and an effort frontier production function is estimated for selected Norwegian fisheries. This makes it possible to estimate optimal vessel size and capital intensity. Fishing vessels appear to be undersized but not too capital intensive.

HANNESSON, R. 1983. Bioeconomic production function in fisheries: theoretical and empirical analysis. Can. J. Fish. Aquat. Sci. 40: 968–982.

L'« effort de pêche », l'approche traditionnelle de l'économique des pêches sous-entend l'existence d'une fonction production, les variables indépendantes étant l'effort de pêche et l'abondance du poisson. Nous démontrons que l'existence d'un équilibre bioéconomique dépend de la forme de cette fonction production, de même que des fonctions demande et coût de l'effort. La présente analyse fait pendant à une discussion récente des affaissements qui se sont produits dans certaines pêches, conséquences d'une accessibilité du poisson inversement reliée à son abondance. Nous estimons, pour la pêcherie des Lofoten, une fonction production de Cobb–Douglas, l'effort et la biomasse de poissons étant les variables indépendantes. Ces calculs indiquent que le coefficient d'accessibilité augmente à mesure que décline le stock de poissons. Finalement, nous intégrons l'approche de l'effort de pêche à une analyse de production néo-classique. Cet effort est considéré comme étant le fruit de la main-d'oeuvre et du capital, et une fonction production à effort limite a été estimée pour certaines pêcheries norvégiennes. On peut ainsi estimer l'optimum de taille des bateaux et d'intensité de capital. Les bateaux semblent trop petits, mais ne sont pas trop intensifs en capital.

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THE standard approach of fisheries economics relates the catch of fish to the application of fishing effort and the abundance of the exploited fish stock. In applied studies it is usually assumed that the catch (y) is proportional to effort (E) and fish biomass (W):

$$(1) \quad y = qEW$$

where q is a constant, referred to as the availability or catchability coefficient (cf. Bell 1972; Clayden 1972; Hannesson 1974; Tomkins and Butlin 1975). This particular specification has its roots in fisheries biology where it serves two purposes. First, the catch per unit of effort (y/E) can be used as an index of fish abundance (W), provided that (1) is valid. Second, having estimated fish abundance, it is possible to predict the catch resulting from any given application of effort. The validity of (1) rests on two foundations. First, one must find a definition of fishing effort that is proportional to the mortality generated in a fish stock of a hypothetical size and distribution; second, the density of fish must be proportional to abundance.

The fishing effort approach and its manifestation in (1) can be criticized in two ways. One concerns the restrictive character of (1) and the other that the concept of fishing effort lacks foundation in the economics of production. First, the specification in (1) is considered. There are strong indications that the availability coefficient is not always constant. In recent years the near collapse of certain fish stocks (e.g. the Atlanto-Scandian herring, the Southwest African pilchard) has been of concern. Fisheries biologists have belatedly ascribed this to an inverse relationship between size and density of the fish stocks in question (cf. Ulltang 1976, 1980; Butterworth

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1981). The fact that the collapse occurred rather suddenly without an "early warning" fall in the catch per unit of effort provides a clue that this is indeed the case.

Why, then, would there be an inverse relationship between q and W? From (1) it is seen that the availability coefficient expresses the catch per unit of effort as a proportion of the exploited stock ($q = (y/E)/W$). As a first approximation, suppose that the catch per unit effort is determined simply by the density of the fish stock. Then, if a declining stock maintains its density by occupying an ever smaller area, the catch per unit of effort will remain "high," and q will be inversely related to W. A similar effect would be produced by gear saturation.

So, instead of (1), a more flexible bioeconomic production function is required where biological (W) and economic (E) factors of production are considered explicitly. The remarks above suggest that the shape of this function is an important determinant of the viability of fish stocks exploited under free access. This is indeed so. In his review and generalization of the earlier literature, Berck (1979) showed that the possibility of extinction depends on whether the smallest viable stock (W^*) is larger or smaller than the minimum stock worthy of exploitation (W^{**}). Extinction is possible if $W^{**} < W^*$; otherwise it is not. As will be shown in the next section, W^* depends on the growth function of the fish stock, while W^{**} depends on the production function together with the demand for fish and the cost of fishing effort. Berck overstated his case, however, when he suggested (p. 881) that the shapes of the harvest cost function (which depends on the production function, the demand function, and the cost function of effort) and the fish growth function are unimportant in the analysis of extinction. While extinction may be possible, it will be much less likely to occur if a (stable) bioeconomic equilibrium exists. In the next section I will show how certain shapes of the growth function, the production function, the demand function, and the effort cost function imply the existence of bionomic equilibria in cases where $W^{**} < W^*$.

In the third section, a first step is taken towards relaxing the restrictive form of (1) by replacing it with a Cobb–Douglas type of function. This function preserves the multiplicative form of (1), which is reasonable, while permitting the availability coefficient to vary with effort and fish abundance. As an illustration, a Cobb–Douglas function is estimated for the Lofoten fishery. In view of the above discussion, the focus is on whether the availability coefficient varies with the abundance of fish. There is some indication of this, and this finding receives further support from the results of the following section.

A major shortcoming of the Cobb–Douglas function in the third section is that it does not allow one to identify the optimal size of fishing vessels. This is related to the second criticism already voiced against the fishing effort approach, namely its weak link to the theory of production. Economic analysis requires that the use of actual inputs (labor, capital, etc.) for which costs are incurred be related to production and revenue. The concept of fishing effort may still be useful, since the catch of fish depends on the abundance of fish stocks and the degree of exploitation. Fishing effort then becomes a fictitious intermediate output synonymous with the degree of exploitation, produced by labor, capital, and other inputs. This type of analysis, integrating the traditional fishing effort approach and conventional production analysis, is conspicuously absent from the literature. This is the subject of the last section of the paper. Here, a neoclassical frontier production function is estimated for some Norwegian fisheries, with labor, capital, and fish abundance as factors of production. This type of analysis allows one to consider questions such as scale economies and optimal capital intensity of fishing vessels, in addition to how the availability coefficient depends on the abundance of fish.

Existence of Bionomic Equilibrium

The phrase "bionomic equilibrium," apparently coined by Gordon (1954), is long since established for a situation in which the biological and economic forces acting upon a fishery simultaneously balance. I shall use the standard technique of deducing two equilibrium loci, one for the biological and another for the economic sphere, and examine the possibility of their intersecting to determine whether a bionomic equilibrium exists.

Equilibrium in the Biological Sphere

Equilibrium in the biological sphere requires that there be zero net growth of the fish stock; i.e. whatever is being removed by fishing during a given period equals the surplus growth (i.e. gross growth minus natural decay) of the fish stock. Denoting surplus growth by G, I shall assume the existence of a growth function that can be written in general terms as

$$G = G(W) = g(W)W \tag{2}$$

where g is the relative growth rate. (It will frequently be easier to interpret the results by reference to the relative growth rate.) Figure 1 shows some possible growth functions whose difference in shape will turn out to be quite important. The equilibrium condition in the biological sphere then is obtained by setting (2) equal to (1), regarding the availability coefficient as a function of E and W in the general case

$$g(W)W = Eq(E,W)W. \tag{3}$$

After dividing both sides by W, differentiation of (3) gives the slope of the biological equilibrium locus in the W,E space:

$$\frac{dE}{dW} = \frac{g' - Eq_W}{q + Eq_E} \tag{4}$$

where the prime denotes derivative and subscripts denote partial derivatives with respect to the argument indicated.

Equilibrium in the Economic Sphere

With free access to the fish stock, the economic equilibrium condition is that the value of the catch per unit of fishing effort be equal to the cost of the marginal effort unit, provided that fishing effort is measured in units of equal efficiency.

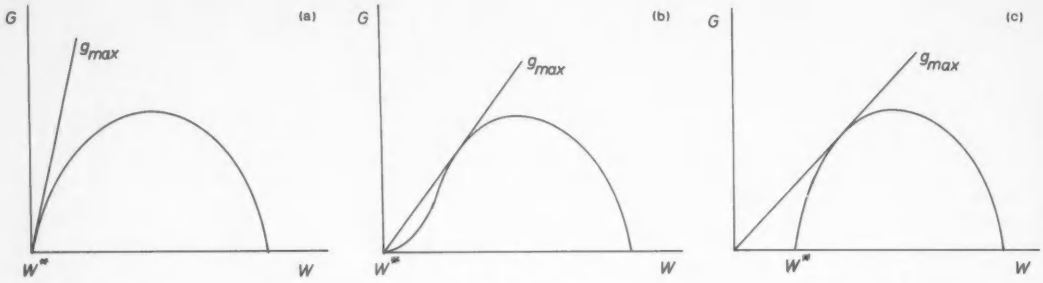

FIG. 1. Three types of growth functions of fish stocks. W^*, the lowest viable population level; g_{max}, maximum relative growth rate.

Denoting the price of fish by p and the cost of the marginal effort unit by c, we obtain

$$p(y)y/E = c(E)$$

or, using (1):

$$(5) \quad p(y)q(E,W)W = c(E),$$

which upon differentiation gives the slope of the economic equilibrium locus in the W,E space:

$$(6) \quad \frac{dE}{dW} = \frac{(q + Wq_W)p(1 + yp'/p)}{c' - W[pq_E + qWp'(q + Eq_E)]}.$$

Bionomic Equilibrium when Price, Cost per Unit Effort, and Availability are All Constant

In this case, (4) becomes

$$(4') \quad \frac{dE}{dW} = \frac{g'}{q}$$

whereas (6) is not defined, but the slope of the economic equilibrium locus will approach infinity as c', q_E, and p' approach zero. Thus, the economic equilibrium (EE) locus is in this case a vertical line (such as EE in Fig. 2), whose intersection with the W-axis shows the level of the fish stock at which costs equal revenues in the fishery. Depleting the fish stock below this level would create losses in the fishery and initiate a process of withdrawal, whereas the excess of revenues over costs at higher stock levels would encourage entry into the fishery.

The shape of the biological equilibrium (BE) locus depends, as can be seen from (4'), on the term g'. When the relative growth rate (g) of the fish population is a monotonically falling function of its abundance, as implied by the growth curve in Fig. 1a, the locus will be negatively sloped. Figure 2 illustrates one such case.[1] But when the relative

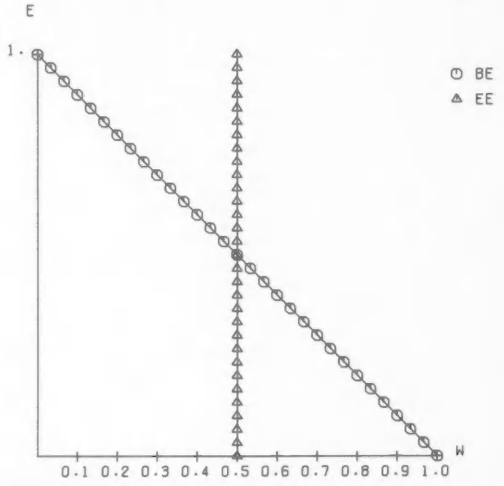

FIG. 2. Biological (BE) and economic (EE) equilibrium loci when the price of fish, cost per unit of effort, and the availability coefficient are all constant and the growth function is as in Fig. 1a.

growth rate of the fish stock is an increasing function of its abundance over some range, as is the case for the growth functions in Fig. 1b–c, the term on the right-hand side of (4') will be positive for small values of W. The BE locus will then be hump shaped, such as the one shown in Fig. 3, and it will have two points of intersection with the positive portion of the W-axis if the growth curve is similarly characterized, as is the case in Fig. 1c. The EE locus may then intersect the W-axis to the left of the BE locus. In that case the stock level at which exploitation is no longer profitable and effort stops expanding (W^{**}) is below the lowest viable level of the population (W^*), and extinction is not only possible but inevitable. From (5) it can be seen that a "high" price of fish or a "low" marginal cost of effort would be responsible for this; the fishery would collapse under its own profitability, as it were.

Relaxing the assumptions of a constant price, availability, and cost of effort may so bend the EE and BE loci as to make them intersect even if $W^{**} < W^*$. A bionomic equilibrium

[1]The equilibrium loci in Fig. 2 and subsequent figures were generated by a simple bioeconomic model, the details of which are given in Appendix 1.

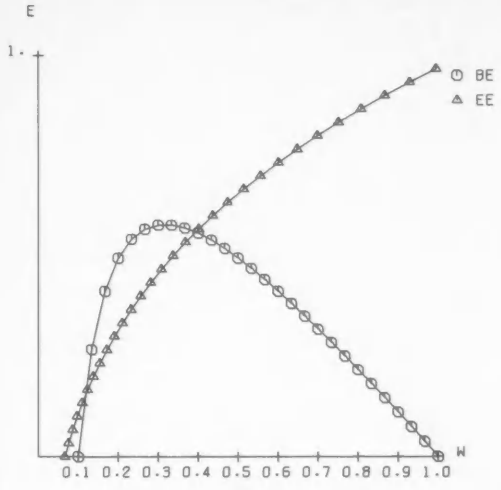

FIG. 3. BE and EE loci when the growth function is as in Fig. 1c and the cost per unit of effort increases with effort.

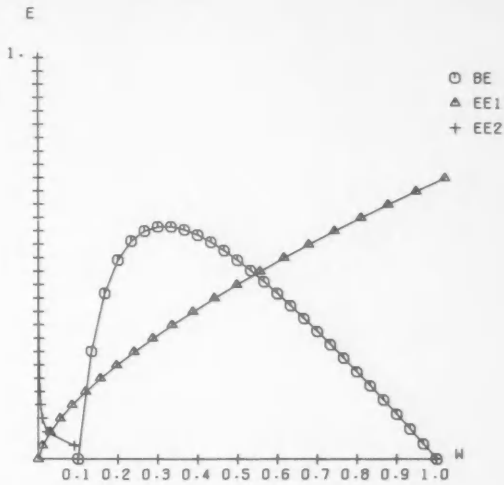

FIG. 4. BE and EE loci when the growth function is as in Fig. 1c and the price of fish varies with the quantity caught. Case 1, elastic demand; case 2, inelastic demand.

then exists, and the probability if not the possibility of extinction will be reduced. This will be discussed further.

Increasing Marginal Cost of Fishing Effort or a Downward Sloping Demand Curve for Fish

The slope of the BE locus remains unaffected by assuming cost and demand curves that are not horizontal. For the slope of the EE locus we have the following expressions:

$$\frac{dE}{dW} = \frac{qp}{c'} \text{ for } c' > 0,\ p' = 0$$

$$\frac{dE}{dW} = -\frac{p(1 + yp'/p)}{W^2 qp'} \text{ for } c' = 0,\ p' < 0. \tag{6'}$$

Dealing first with the case where $c' > 0$, it is seen that the slope of the EE locus is positive, and decreasing if $c'' > 0$. It is possible that a bionomic equilibrium will exist, even if the EE locus intersects the W-axis to the left of the BE locus. A case such as this is shown in Fig. 3 where, in fact, two bionomic equilibria exist, the one in the positively sloping portion of the BE locus being unstable. Intuitively this result is easy to understand; an increasing marginal cost of fishing effort will retard its expansion and thereby make it less likely that the fish population will be depleted below its lowest viable level.

As for the case where $p' < 0$, the sign of dE/dW is ambiguous, depending on whether the term yp'/p is greater or smaller than -1. This term is recognized as being the inverse of the elasticity of demand. Elastic demand implies that the numerator of (6′) will be positive ($yp'/p > -1$), and since the denominator is negative, the right-hand side of (6′) will be positive. The EE curve will be positively sloped, such as EE1 in Fig. 4, with similar implications for the existence of bionomic equilibrium as a rising marginal cost of fishing effort. Inelastic demand reverses the sign of (6′), and the EE locus becomes negatively sloped, such as EE2 in Fig. 4. The starting point of this locus corresponds to a floor price at which demand suddenly becomes infinitely elastic. I have placed this starting point to the left of the BE locus so that no bionomic equilibrium would exist if this price limit were always binding. A price increase, due to reduced catches, would raise revenues and provide an incentive for expanding fishing effort and a further depletion of the fish stock. This explains the negative slope of the EE2 locus. Inelastic demand thus increases the probability of extinction, contrary to elastic demand.

Availability Coefficient Dependent on the Fish Stock Level

If the availability coefficient varies with the level of the exploited fish population, this will affect the slope of both equilibrium loci. Since the slope of the EE locus is not defined when both p and c are constant, I shall assume that one of these is variable. This gives

$$\frac{dE}{dW} = \frac{g' - Eq_W}{q} \tag{4''}$$

$$\frac{dE}{dW} = \frac{(q + Wq_W)p}{c'} \text{ for } c' > 0,\ p' = 0$$

$$\frac{dE}{dW} = -\frac{(q + Wq_W)p(1 + yp'/p)}{W^2 q^2 p'} \text{ for } c' = 0,\ p' < 0. \tag{6''}$$

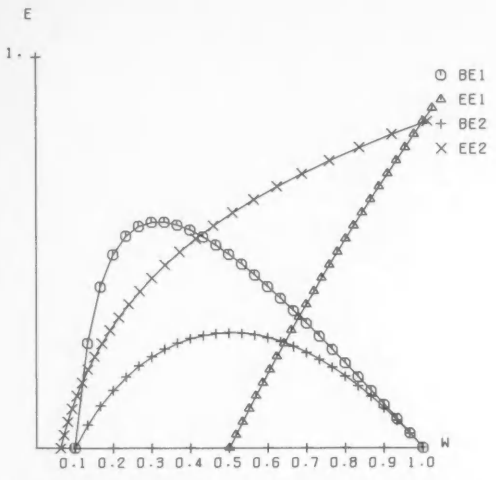

FIG. 5. BE and EE loci when the growth function is as in Fig. 1c. Case 1, constant availability coefficient; case 2, availability coefficient rises as the stock is depleted.

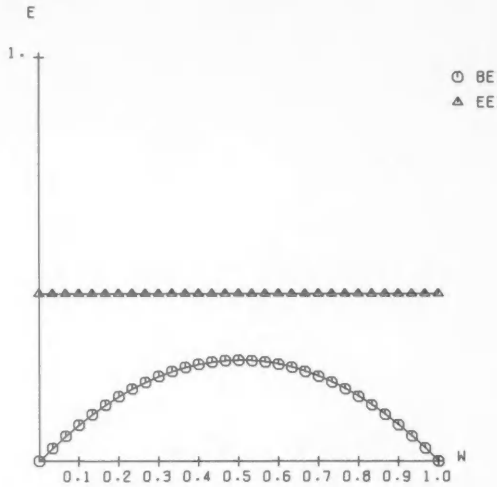

FIG. 6. BE and EE loci when the catch per unit of effort is independent of stock density (size) and either the demand for fish is elastic or the cost per unit of effort rises with effort.

To show clearly the implications of a variable availability coefficient, I shall compare two fish populations that are identical in every respect, except that one of them is characterized by a variable availability coefficient. The availability coefficient will be assumed to have the same value for both populations in natural equilibrium. Alternatively, one may think of this in terms of comparing two different methods of exploiting one fish population, these being characterized by a constant versus variable availability coefficient.

Curve BE1 in Fig. 5 shows the BE locus for the population with constant availability, while Curve BE2 refers to the other population. Both loci must intersect the W-axis in the same places, since both populations are characterized by the same growth function. Since $q_W < 0$, locus BE2 will be less steep than BE1 in its negatively sloping portion and attain maximum at a higher value of W. Therefore, locus BE2 will lie below BE1 everywhere, as shown in Fig. 5.

As to the EE loci, which are numbered in the same way, the sign of their derivatives is ambiguous in the case where $p' < 0$. Assuming elastic demand, these loci will be positively sloped, intersecting at the natural equilibrium level of the respective fish population because both populations are then characterized by the same availability. From (6″) it can be seen that the EE locus for the population characterized by a constant availability coefficient must be steeper than the other because the negative term Wq_W appears in the numerator of (6″).

Comparing the equilibrium loci for the two populations, it is seen how a stock-dependent availability coefficient reduces the chances that a bionomic equilibrium will exist. Loci EE1 and BE1 intersect, while EE2 and BE2 do not, and so there exists no bionomic equilibrium for the population with the variable availability coefficient. It is easy to understand why. The mechanism prohibiting an irreversible depletion of fish stocks by a free-access fishery simply is the lack of profitability to do so; the continued existence of an exploited fish population is possible only if the incentives to a further depletion have been exhausted before it has been reduced below its threshold level of viability. When the availability coefficient varies inversely with the abundance of fish ($q_W < 0$) this mechanism is weakened; the catch per unit of fishing effort will not fall as rapidly when the fish population is depleted as it otherwise would, and a fishery that is profitable at high levels of fish abundance will remain so even at much lower levels of abundance. The most extreme case is when the catch per unit of fishing effort is totally insensitive to the size of the fish population ($q + Wq_W = 0$), as is often supposed to be the case for pelagic species that form shoals and are caught by purse seining, suitable shoals being possible to find at almost constant cost until nothing is left. The right-hand side of (6″), then, is zero, and the EE locus will be a horizontal line (as shown in Fig. 6), its point of intersection with the E-axis being determined by (5). Since the catch per unit of effort is constant in this case, either the cost per unit of effort will have to rise or the price of fish will have to fall as effort (and thereby total catch) expands, in order that the EE line be defined. If these forces are not strong enough, the EE locus will lie above the BE locus, as in Fig. 6, and the fish population will be driven to extinction even though its lowest viable level is infinitesimally small; while $W^* = 0$, W^{**} (the smallest population worthwhile to exploit) is not defined.

Availability Coefficient Depending on the Level of Fishing Effort

Here, it is assumed that c', p', and q_W are all zero, since the slope of the EE locus nevertheless will be defined. Equations (4) and (6) then become

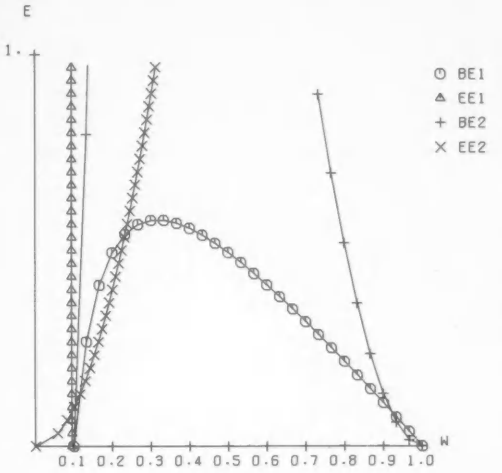

FIG. 7. BE and EE loci when the growth function is as in Fig. 1c. Case 1, constant availability coefficient; case 2, availability coefficient decreases as effort increases (negative crowding externalities).

$$(4''') \quad \frac{dE}{dW} = \frac{g'}{q + Eq_E}$$

$$(6''') \quad \frac{dE}{dW} = -\frac{qp}{Wpq_E}.$$

To clearly see the implications of this, two technologies are compared, one characterized by a constant availability coefficient and the other not. First, suppose that the availability coefficient is the same for both technologies at some "low" level of fishing effort, but that one technology is characterized by diminishing returns to fishing effort ($q_E < 0$). At higher levels of fishing effort the slope of the BE locus will be steeper for the technology with diminishing returns. This is shown in Fig. 7; locus BE1 refers to the technology with constant returns (note that I have cut the top off the BE2 locus).

The EE locus will, for constant returns, be a vertical line, such as EE1 in Fig. 7, as already explained. With nonconstant returns, its derivative will be defined and will be positive when the returns to fishing are diminishing, as shown by EE2 in Fig. 7. Note that EE1 and EE2 intersect at the effort level where the availability coefficient is the same for both technologies.

Comparing the equilibrium loci for the two technologies shows that EE2 and BE2 intersect, while the others do not. Diminishing returns will therefore increase the possibility that a bionomic equilibrium exists. The reason is quite obvious; diminishing returns to fishing effort imply that expansion of fishing effort will not be as profitable as otherwise, and the depletion of fish stocks through excessive effort will be less likely to occur. Increasing returns to fishing effort would reverse the argument.

A Bioeconomic Production Function with a Variable Availability Coefficient

As a step towards finding a more flexible function to replace (1), I suggest that the catch of fish be considered as a product of two functions:

$$(7) \quad y = \psi(E)\Omega(W).$$

The impact of fishing effort on a stock of a hypothetical size and distribution is given by the function ψ; in the absence of crowding externalities of any kind, this function would be linear. The fishing mortality generated by ψ may depend on the abundance of fish, for reasons mentioned in the introduction. This would be reflected by the function Ω. A simple form of (7) is the Cobb–Douglas function:

$$(8) \quad y = AE^{\mu}W^{\nu}$$

where A is constant.
Estimating the parameters μ and ν then allows the determination of whether the availability coefficient is constant or not. The availability coefficient implied by (8) is

$$(9) \quad q = AE^{\mu-1}W^{\nu-1}.$$

The availability coefficient would thus be constant if μ and ν are both equal to one. If the density of the stock decreases less than proportionally with the size of the stock, then q will be inversely related to W, and we have $\nu < 1$. As to how μ might deviate from one, it is noted that $\mu < 1$ would imply congestion externalities and $\mu > 1$ the opposite. To the extent that any such externalities are present, one might expect $\mu > 1$ for "few" vessels and $\mu < 1$ for "many." This specification only allows a constant μ, however. This is probably not a problem in the case about to be presented because fishing effort varies rather moderately from year to year but shows a strong time trend.

As a case in point, (8) was estimated for the Lofoten winter cod fishery using data covering the years 1950–78 (Lofotfisket (The Lofoten Fishery) Annual Reports 1950–78, Norwegian Directorate of Fisheries, Bergen). The information that comes closest to referring to fishing effort is participation in terms of men and boats at the end of each week in the season. I have calculated fishing effort as the sum of boats or, alternatively, fishermen across weeks, and thus have two effort variables referred to as man-weeks and boat-weeks, respectively. The data on fish biomass have been taken from the 1980 report of a working group of the ICES (1980a). This report contains estimates of the size of the various cohorts of the Arcto-Norwegian cod stock, the spawning part of which is the main resource exploited by the Lofoten winter cod fishery. I have calculated the biomass of the spawning stock as the total weight of all cohorts aged 8 yr or more.

Since some technological change has probably occurred in the fishery during the period considered, (8) must be reformulated to be consistent with this. By assuming an exponential rate of technological change, the following expression is arrived at:

TABLE 1. Results of estimating the equation $\frac{y_{i,t+1} - y_{i,t}}{\frac{1}{2}(y_{i,t} + y_{i,t+1})} = \gamma_i + \mu_i \frac{E_{i,t+1} - E_{i,t}}{\frac{1}{2}(E_{i,t} + E_{i,t+1})} + \nu_i \frac{W_{t+1} - W_t}{\frac{1}{2}(W_t + W_{t+1})}$. Data below μ and ν show, respectively, the point estimate, the t-value, and the critical probability value for accepting the hypothesis that the parameter equals one (for ν a one-sided t-test was applied). Data below F show the critical point at the 5% level.

	N	$\mu\cdot\gamma$	μ	ν	F	R^2	$D-W$
Gill nets							
Man-weeks	26	0.0443	0.9621	0.7707	12.47	0.52	2.64
			(2.86)	(3.43)	(3.44)		
			>0.5	0.15			
Boat-weeks	28	0.0348	0.8133	0.7957	11.87	0.49	2.70
			(2.59)	(3.58)	(3.40)		
			>0.5	0.18			
Longline							
Man-weeks	26	0.0472	0.8379	0.8284	14.08	0.55	2.54
			(2.64)	(4.07)	(3.44)		
			>0.5	0.20			
Boat-weeks	28	0.0596	0.9028	0.8445	16.66	0.57	2.59
			(3.02)	(4.46)	(3.40)		
			>0.5	0.21			
Handline							
Man-weeks	26	0.0232	0.2197	0.8637	6.29	0.35	2.18
			(0.87)	(2.67)	(3.44)		
			0.003	>0.25			
Boat-weeks	28	0.0193	0.3811	0.8165	7.60	0.38	2.47
			(1.35)	(2.72)	(3.40)		
			0.037	>0.25			
Danish seine							
Man-weeks	19	−0.1434	1.3542	0.8940	2.30	0.22	2.72
			(2.07)	(1.24)	(3.63)		
			>0.5	>0.25			
Boat-weeks	19	−0.1339	1.4154	0.9011	2.94	0.27	2.54
			(2.36)	(1.30)	(3.63)		
			>0.5	>0.25			
Aggregate							
Man-weeks	26	0.0735	1.0188	0.7434	22.35	0.66	2.19
			(4.08)	(4.26)	(3.44)		
			>0.5	0.08			
Boat-weeks	28	0.0339	0.9511	0.7806	30.08	0.71	2.36
			(4.99)	(5.08)	(3.40)		
			>0.5	0.08			

(10) $y_{it} = A_i E_{it}^{\mu_i} W_t^{\nu_i} e^{\gamma_i t} u_{it}$

where subscript t refers to time (1949 = 0), i refers to the type of fishing gear, and u is an error term. A multiplicative error term is more reasonable than an additive one. For example, if adverse natural conditions prohibited the effective application of fishing effort for some part of a particular week, this would, according to (8), affect catches by some fraction of fishing effort *multiplied by* the level of biomass to which it would have been applied under normal conditions. There are mainly four types of gear to be considered: gill nets, longline, handline, and Danish seine. The aggregate fishery is also considered, after having constructed an aggregate fishing effort variable. The aggregation procedure is described in Appendix 2.

Equation (10) is unsuitable for estimation because of a strong time trend in W (the correlation between W and t is −0.81). Differentiating (10) with respect to time (superior dots denote time derivatives) gives

$$\frac{\dot{y}_{it}}{y_{it}} = \gamma_i + \mu_i \frac{\dot{E}_{it}}{E_{it}} + \nu_i \frac{\dot{W}_t}{W_t} + \frac{\dot{u}_{it}}{u_{it}}.$$

This was estimated by a linear regression, approximating relative changes by

$$\frac{y_{i,t+1} - y_{i,t}}{\frac{1}{2}(y_{i,t} + y_{i,t+1})}$$

and analogous for E and W. The results are summarized in

Table 1. The absence of serial correlation indicated by the Durbin–Watson statistic lends support to the idea that estimating (7) is a meaningful exercise, although it is really only one equation of a three-equation structural model in which W and E are endogenous as well as y. Regarding E and W as exogenous variables may be defended as follows. The Lofoten fishery exploits mature year classes of cod, the size of the exploited stock in any particular year being determined to a large extent by the size of the new mature year class. The feedback between the rate of exploitation and the exploitable stock is therefore weak in this particular fishery. As to fishing effort, the year to year fluctuations are very moderate, but there is a strong time trend.

What do the results in Table 1 suggest with respect to the hypothesis of a constant availability coefficient? For μ the null hypothesis $\mu = 1$ is acceptable at any reasonable level of significance, except for handline boats, for which μ is surprisingly low. It is unlikely that there are strong crowding externalities among these vessels but not others. A possible explanation is that marginal handline boats are much less efficient than the rest. The significance of the regression for handline boats is rather low, however.

As for ν, it is easier to reject the null hypothesis $\nu = 1$. In view of the previous discussion the alternative hypothesis is $\nu < 1$, and thus a one-tailed test of significance is appropriate. For the aggregate fishery one would reject $\nu = 1$ at a 10% level of significance, and for gill nets and longline one would do so at the 15–20% level. For the handline and Danish seine vessels one would accept $\nu = 1$ at any reasonable level of significance, but the F values of these regressions are very low. Considering that all point estimates of ν are below one, there seems to be an indication that the true value of ν is indeed below one. The availability coefficient thus appears to increase slightly as the abundance of fish decreases. The catch per unit of effort is influenced by fish abundance ($\nu > 0$) but not to the extent implied by a constant availability coefficient ($\nu = 1$).

The estimated values of γ indicate a technological progress of 2–7% per year ($\nu\gamma$). The exception is the Danish seine vessels, for which the results imply a technological regress of more than 10% per year. This nonsensical result further undermines the confidence one might have in the regressions for this group of vessels.

Integration of the Fishing Effort Approach and Neoclassical Production Analysis

Production studies in the neoclassical spirit focus on questions such as optimal size and capital intensity of production units. These are obviously no less relevant for the fishery than other industries. In the context of fisheries, a satisfactory specification of the production function is likely to involve explicit consideration of the fish resource, as the results of the previous section indicate. As an illustration of how one might go about this, an analysis of frontier production functions in selected Norwegian fisheries is presented. The data used and manipulation of these are presented in Appendix 3.

In addition to the fish stock (W), the classic factors labor (L) and capital (K) shall be considered. The general form of the production function is

$$(11) \quad y = \varphi(K,L,W).$$

If (11) is (weakly) separable in the arguments K and L on the one hand and W on the other, (11) may be written as

$$(11') \quad y = \varphi(\phi(K,L),W)$$

where ϕ may be regarded as a production function of fishing effort. Circumstances under which (11) would not be separable can be imagined. Suppose, for example, that fish stocks become more difficult to locate the further they are depleted. This would increase the comparative advantage of vessels equipped with fish-finding devices. It will be assumed that (11) is separable (see Appendix 4 for a test of this) and multiplicative (cf. beginning of the previous section), so that (11) can be written as

$$(12) \quad y = \phi(K,L)W^{\nu}.$$

Note that, if ϕ is taken to be the production function of effort (as will be done), it does not correspond to the function $\psi(E)$ in (7). Here, $\psi(E) \equiv 1$ in (7), and crowding externalities are ignored, partly on the basis of the results in the previous section.

A Stochastic Cobb–Douglas Frontier Function

The following assumptions are made for the function ϕ: (i) it is of the Cobb–Douglas type, but not necessarily characterized by constant returns to scale (see Appendix 4 for a discussion of the validity of this specification) and (ii) technological progress is neutral and occurs at an exponential rate. This gives

$$(13) \quad \phi(K,L,t) = Ae^{\lambda t} L_t^a K_t^b$$

where λ is the rate of technological progress and t denotes time measured in years.

A frontier function reflects technological possibilities ex ante rather than substitution possibilities ex post (see Johansen 1972). All inefficient fishing vessels were thus excluded from the sample. An inefficient vessel is defined as one that produced less than another some particular year while using more of labor or capital and not less of either. Initially, the possibility that the observed input coefficient of an efficient vessel may lie on either side of the frontier isoquant[2] will be allowed for, as would be the case if the output variable were measured with an error. There is some reason to believe that this is so in this case. Output is defined as the value of landings per day at sea, but the number of days at sea may be incorrectly reported, and more importantly, all days at sea are not equal in terms of conditions for fishing. More precisely, it is assumed that (13) is multiplied by an error term u whose logarithm has an expected value of zero and a constant variance. Inserting (13) into (12) and taking logarithms gives the

[2] The term "isoquant" is used by economists for the locus of points showing all combinations of inputs yielding a given output, provided that the production is technologically efficient.

TABLE 2. Results of estimating (14). Data in parentheses show t-values. Data with an asterisk (below ν) show the critical probability values for rejecting the hypothesis that $\nu = 1$ (one-tailed test).

Fishery	Exploited stock	Gear used	N (vessels)	λ	a	b	ν	R^2	F
1	Saithe, age 3–7	Any	131	0.0227 (0.87)	1.1242 (10.62)	0.8197 (10.70)	0.7034 (2.31) 0.16*	0.78	114.2
2	Arcto-Norwegian cod, age 5–8	Any	58	0.0415 (0.68)	1.6166 (7.10)	−0.1507 (0.71)	0.6380 (2.16) 0.11*	0.66	25.6
3	Arcto-Norwegian cod, age 8+	Gill nets	109	−0.0046 (0.17)	1.0733 (10.20)	0.6973 (9.04)	0.8684 (6.98) 0.14*	0.80	104.7
4	Arcto-Norwegian cod, age 8+	Longline, excluding "bankline"	61	0.0832 (2.68)	1.0082 (6.89)	0.3160 (2.78)	0.8574 (5.86) 0.16*	0.81	60.2
5	Arcto-Norwegian cod, age 8+	Danish seine	26	0.0485 (0.40)	2.0157 (3.74)	0.8838 (1.16)	0.5394 (1.00) 0.20*	0.48	4.8
6	Arcto-Norwegian cod, age 4–7	Trawl, Barents Sea + Spitsbergen	45	0.0103 (0.46)	−0.3449 (1.10)	0.7910 (4.55)	0.0108 (0.09) <0.001*	0.49	9.7

function to be estimated:

$$(14)\quad \ln y_{it} = \ln A + \lambda t + a \ln L_{it} + b \ln K_{it} + \nu \ln W_{it} + \ln u_{it},$$

where subscript i refers to vessel i.

The results of estimating (14) by ordinary regression are shown in Table 2. There are three important economic implications to be noted: technological progress, the output elasticity of the fish stock, and returns to scale at the vessel level.

First, there is little evidence of technological progress. The estimated values of λ are all insignificant, except for fishery 4. Here, the rate of technological progress is as high as 8% per year and stands in marked contrast with the estimates for fisheries 3 and 5, which involve vessels of a similar size exploiting the same fish stock but using a different type of fishing gear. There is evidence, however, against the validity of the Cobb–Douglas function for fishery 4 (cf. Appendix 4).

Second, all the point estimates of ν are below one. This agrees with the results in the preceding section in indicating that the catch per unit of effort increases less than proportionally with the abundance of fish, but it is difficult here as well to refute statistically the hypothesis that $\nu = 1$ (the critical probability values for a one-tailed test fall between 0.10 and 0.20), except for the trawl fishery (fishery 6). The low value of ν estimated for this fishery is indeed surprising, as it indicates that the abundance of fish has no influence whatsoever on the output per unit effort.

Third, there is the question of returns to scale at the vessel level. Sato (1980) pointed out the impossibility of distinguishing between scale effects and a uniform factor-augmenting technical progress in time-series analyses of homothetic production functions such as (13). When using cross-sectional data, returns to scale would be reflected through the sum of a and b. Here, a time series of cross-sectional data is used giving reason to believe that the sum of a and b will reflect returns to scale, while "technical progress," whether of the factor-augmenting variety or due to changing returns to scale over time, would show up in the term $e^{\lambda t}$. Earlier estimates of the function to be specified presently (17) from cross-sectional data for 1 yr alone showed pervasive economies of scale (cf. Hannesson et al. 1981). For all fisheries except 2 and 6 the sum of a and b is greater than one, implying increasing returns to scale. For fisheries 2 and 6 the estimated value of one of these coefficients is negative and meaningless, but for fishery 2 the returns to labor are increasing.

A Deterministic Homothetic Frontier Function

One of the shortcomings of the Cobb–Douglas function is the impossibility of identifying the optimal size of production units on the basis of its parameters. One particular specification that extends the Cobb–Douglas function to the case where the elasticity of scale depends on the level of output is from Zellner and Revankar (1969). They constructed a homothetic production function by applying a transformation function (g) to a neoclassical production function of an arbitrary degree of homogeneity (f). Applying this transformation to the production of fishing effort yields

$$(15)\quad E = g(f(K,L)).$$

Assuming that the function (f) is Cobb–Douglas and homogeneous of degree γ gives

$$(16)\quad f(K,L) = AL^{\gamma\delta} K^{\gamma(1-\delta)}.$$

Zellner and Revankar did not specify the function $g(f)$ but proceeded instead by defining and specifying a returns-to-scale function, $h(g)$. Following their procedure, (15) can be written as (cf. Zellner and Revankar 1969, p. 242 ff.)

$$(17)\quad E^{\alpha}e^{\beta E} = A^{*}L^{\delta}K^{1-\delta}$$

where α and β are parameters and $A^{*} = A^{1/\gamma}$. Note that the intermediate output E corresponds to the output variable in Zellner and Revankar's framework.

Equation (17) makes it possible to identify vessels of an optimal size. The elasticity of scale is

$$(18)\quad \epsilon = 1/(\alpha + \beta E),$$

and thus the optimal vessel is given by $E = (1 - \alpha)/\beta$. This identifies an isoquant in the L,K plane, leaving one degree of freedom for the relevant factor price ratio to determine the optimal combination of L and K.

Technological change may manifest itself in two ways. The returns-to-scale function may shift over time, which can be accounted for by letting α and β be time dependent (cf. Førsund and Hjalmarsson 1979). Attempts to estimate linear time trends in these parameters were unsuccessful in this case, and hence, the returns-to-scale function shall be regarded as independent of time. Second, technological progress may affect the kernel function (16). Assuming that this occurs in a Hicks-neutral way at a constant exponential rate amounts to multiplying (16) by an exponential term to give

$$(19)\quad E^{\alpha}e^{\beta E} = A^{*}e^{\lambda t}L^{\delta}K^{1-\delta}.$$

This type of technological progress implies that the amount of scale-optimal effort $[E^{0} = E(\epsilon \mid \epsilon = 1)]$ will be produced by less and less labor and capital as time goes by, given that the returns-to-scale function is independent of time.

For the purpose of estimating (19), fishing effort (E) must be known. This variable is not directly observable, and thus, its implied value, y_i/W_i^{ν} (cf. (12)) was calculated using the ν values estimated by (14). There is reason to believe that these estimates will not be seriously biased. Taking logarithms of $y = EW^{\nu}$ and using (19) yields

$$(20)\quad \ln y = [-\beta E + \ln A^{*} + \delta \ln L + (1 - \delta)\ln K + \lambda t]/\alpha + \nu \ln W.$$

The difference between (14) and (20) is that E is missing in (14). The bias resulting from estimating ν by (14) when (20) is the correct specification will depend on the correlation between $\ln W$ and E. Since E is a function of L and K, we get some idea of this by looking at the correlation between W and K and L. The correlation coefficients are as follows (asterisks indicate significant correlation at the 5% level):

	Fishery					
	1	2	3	4	5	6
Labor	0.09	−0.06	0.08	0.08	0.04	−0.34*
Capital	−0.21*	0.04	−0.24*	−0.02	−0.57*	0.37*

None of these coefficients seems exceedingly high, except perhaps for fisheries 5 and 6. These are also the ones with the lowest and least significant estimate of ν.

The linearized form of (19) is not amenable to the application of linear regression. Instead, the method employed by Førsund and Hjalmarsson (1979) in a study of the Swedish dairy industry was used. This involves treating (19) as a deterministic frontier function, implying that deviations of the input coefficients from the frontier isoquant can only be one sided. Therefore, the left-hand side of (19) must, for every single production unit, be less than or equal to its right-hand side. Taking logarithms gives

$$(21)\quad \alpha \ln E_t + \beta E_t \le \ln A^{*} + \lambda t + \delta \ln L_t + (1 - \delta)\ln K_t.$$

The parameters α, β, A^{*}, λ, and δ can then be estimated by minimizing the sum of differences between the left and right sides. This defines the following linear programming problem:

$$(22)\quad \text{Max} \sum_t \Big(\alpha \sum_{i=1}^{n_t} \ln E_{it} + \beta \sum_{i=1}^{n_t} E_{it} - n_t \ln A^{*} - \lambda n_t t - a \sum_{i=1}^{n_t} \ln L_{it} - b \sum_{i=1}^{n_t} \ln K_{it}\Big)$$

subject to

$$\alpha \ln E_{it} + \beta E_{it} - \ln A^{*} - \lambda t - a \ln L_{it} - b \ln K_{it} \le 0$$

$$a + b = 1,\ \alpha > 0,\ \beta \ge 0,$$

where n_t = number of vessels in year t. The first side constraint is consistent with the assumption that a particular production unit may use its resources inefficiently and produce less output than implied by the frontier function. Errors of measurement, which in fact might show a greater output for some production units than implied by the frontier function, are thus implicitly ignored. The second side constraint follows directly from the specification of the kernel function (16). The third and fourth side constraints imply the plausible assumption that the elasticity of output with respect to the scale of fishing effort (i.e. proportionate variations in L and K) be positive and nonincreasing with effort.

A well-known shortcoming of this method is that the results are sensitive to certain extreme observations and cannot be assessed by any statistical measures of significance. Some indication of their reliability can, however, be obtained by comparison with the results of estimating the Cobb−Douglas function. Since the only difference between (14) and (21) is that the elasticity of scale implied by (21) varies with output, the estimates of both equations should imply the same optimal K/L ratio.

Optimal Vessel Size

Table 3 shows the results of estimating (21). The results in parentheses were obtained by changing the assumed value of

TABLE 3. Results of estimating Equation (21).

Fishery	Assumed value of ν	α	β	δ	λ	ln A^*	Comment	$(1-\delta)/\delta$	b/a (cf. Table 2)
1	0.7034	0.3478	0.00134	0.5197	0	−2.34478	Efficient	0.9242	0.7291
	(0.8)	(0.3862)	(0.00168)	(0.5491)	(0)	(−2.30207)	vessels	(0.8212)	
2	0.6380	0.3188	0.00051	0.5299	0	−2.05662	All vessels	0.8871	—
	(0.7)	(0.3361)	(0.00059)	(0.5429)	(0)	(−2.06972)	(N = 276)	(0.8420)	
3	0.8684	0.3509	0.00088	0.6131	0	−1.86366	Efficient	0.6311	0.6497
	(0.9)	(0.3316)	(0.00135)	(0.6138)	(0)	(−1.98238)	vessels	(0.6292)	
4	0.8574	0.4575	0	0.4347	0	−2.44771	All vessels	1.3004	0.3134
	(0.9)	(0.4500)	(0)	(0.4703)	(0)	(−2.39706)	(N = 142)	(1.1263)	
5	0.5394	0.2073	0	0.6886	0	−1.74062	All vessels	0.4522	0.4385
	(0.6)	(0.2068)	0	(0.6868)	0	(−1.82803)	(N = 61)	(0.4561)	
6	0.0	0.4864	0	1.0	0.0324	2.63073	All vessels	—	—
	(0.5)	(0.4121)	(0)	(1.0)	(0.0482)	(0.22162)	(N = 141)		

ν slightly to ascertain the sensitivity of the results to changes in this parameter. First, consider the elasticity of scale, the variability of which it was the main purpose to investigate by estimating (21). By (18), this will vary with output only if $\beta \neq 0$. Such estimates of β were obtained for fisheries 1−3. For fisheries 4−6, $\beta = 0$ and $\alpha < 1$, which implies that the elasticity of scale is constant and greater than one, indicating a similar tendency to increasing returns-to-scale as the results in Table 2 show. The estimated value of λ is zero in all cases but one, again indicating absence of technological progress.

The optimal size of vessels in fisheries 1−3 compared with the vessels actually in the fleet is most easily shown by isoquant maps (Fig. 8a−c). As explained in connection with (18), optimal scale ($\epsilon = 1$) identifies an isoquant in the K,L plane. The isoquants so identified for fisheries 1−3 are shown in Fig. 8a−c together with the actual input of capital and labor in the 1977 sample of vessels (points marked by ×). From this, it appears that most existing vessels are too small to fully utilize the economies of scale. In fishery 3 (Fig. 8c) there is not a single vessel in the 1977 sample that is large enough for this purpose, while in fishery 1 (Fig. 8a) some of the very largest vessels are. In fishery 2 (Fig. 8b) there is one exceptional vessel (a trawler) that is much larger than needed for attaining an optimal scale, whereas all remaining vessels are too small.

Why is it that almost all vessels appear to be of a suboptimal size? Does this imply that fishermen are irrational in their choices among vessel designs? Not necessarily. Interestingly enough there are very few vessels of overoptimal size in the fisheries for which it proved possible to identify an optimal vessel (fisheries 1−3). Suboptimal vessels would result from constraints on the availability of factors, such as constraints on available credit or the supply of labor. With regard to labor, it is possible that boatowners prefer "small scale" because of easier overseeing and the personal relations among the crew that often characterize this type of activity. Yet another possible explanation is that the returns-to-scale function has been drifting over time, so that economies of scale are being realized with ever larger vessels. This hypothesis was not supported by adding linear trend terms to parameters α and β.

OPTIMAL K/L RATIO

A comparison with the results in Table 2 is facilitated by the last two columns in Table 3. These columns show data related to the optimal capital−labor ratio. Setting the ratio of marginal products of capital and labor equal to their price ratio, the optimal capital to labor ratio ($(K/L)^0$) from (13) and (19) are, respectively,

$$(K/L)^0 = \frac{w}{r}\frac{b}{a}$$

(23)

$$(K/L)^0 = \frac{w}{r}\frac{1-\delta}{\delta}$$

where w and r denote the opportunity costs of labor and capital, respectively.

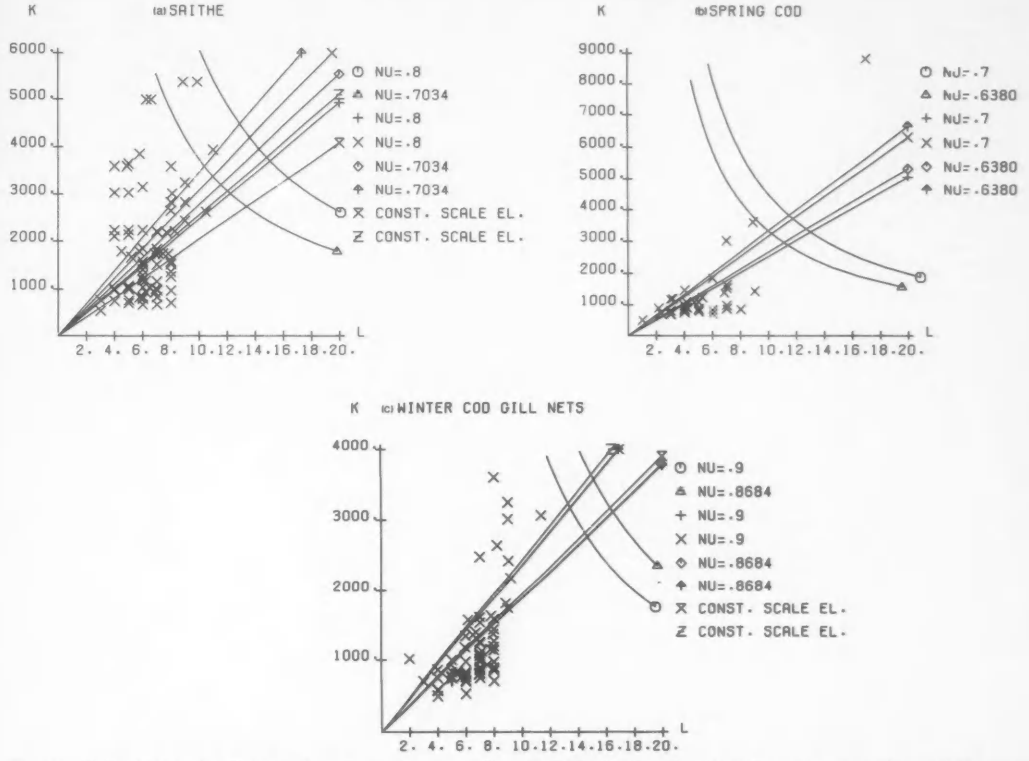

FIG. 8. Optimal size and capital intensity and actual input use of vessels fishing for (a) saithe, (b) spring cod, and (c) winter cod. Curves show isoquants for vessels of an optimal size for two alternative values of ν (output elasticity of the fish stock). Rays show optimal capital intensity of vessels for two alternative wage−capital rent ratios and two production functions, Cobb−Douglas and Zellner−Revankar, the latter with two alternative values of ν. Points marked by × show actual use of inputs by vessels in the 1977 sample.

Comparing the data in the last two columns of Table 3 shows that the parameters of the Cobb−Douglas function (14) and those of the Zellner−Revankar function (21) imply very similar optimal K/L ratios for fisheries 3 and 5, somewhat less so for fishery 1, and strikingly divergent for fishery 4, while for fishery 2 and 6 no such comparison is possible. The optimal K/L ratio is practically unaffected by changing the assumed value of ν in fisheries 3 and 5, while it is more unstable for fisheries 1, 2, and 4. The results of the estimations therefore seem rather satisfactory for fisheries 3 and 5 (except for the elasticity of scale in fishery 5), less so for fisheries 1 and 2, while those obtained for fisheries 4 and 6 merit little further attention.

On the basis of the data in the last two columns of Table 3 and two different assumptions regarding the w/r ratio the optimal K/L ratios have been calculated (cf. (23)). These two w/r ratios were obtained by assuming a 5 and 10% alternative rate of return on capital, respectively, which appears to set reasonable limits. Adding 15% for depreciation and maintenance, which is close to the average figure in the period considered, gives a 20 and 25% gross rate of return. The opportunity cost of labor has been set at 75 000 kroner at 1977 prices, which is close to the average income attained by industrial workers in Norway in 1977. This gives a w/r ratio of 300 and 375, respectively, capital being measured in 1000 kroner. The resulting ratios are shown as straight lines in Fig. 8a−c; note that the two alternative assumptions about the w/r ratio produce two optimal K/L ratios for each value in the last column in Table 3.

Given that loans for investment in fishing vessels have for many years been obtainable on particularly favorable terms, one would expect existing vessels to be characterized by a higher K/L ratio than optimal. Figures 8a−c do not support this hypothesis. The majority of points representing the inputs of labor and capital in the 1977 fleet lie below the lines showing the optimal K/L ratio, indicating that the vessels are on the average too labor intensive. A similar analysis for fishery 5 (not shown) gave the opposite result, however; here, all vessels in the 1977 sample appeared to be too capital intensive.

It is possible that a systematic "bias" in the data has led to biased estimates of the output elasticities, showing the

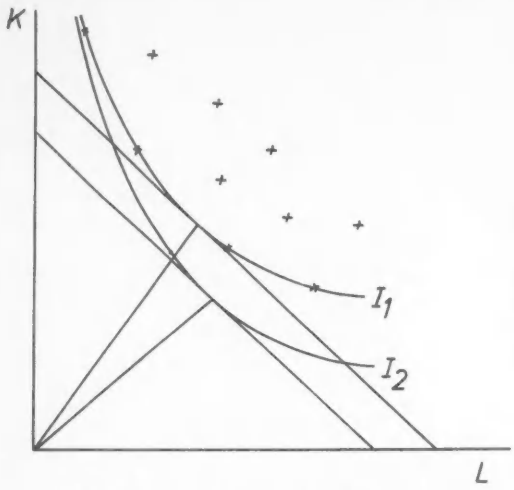

FIG. 9. Consequences of estimating a frontier isoquant from a sample of vessels of different vintages when a neutral technological progress has occurred together with increasing capital intensity. I_2, true isoquant with contemporary technology; I_1, estimated isoquant. Points marked by × show actual observations.

optimal capital to labor ratio to be higher than the true one. Consider Fig. 9. Estimating a deterministic frontier function fits an isoquant such as I_1 to the observed input coefficients (assuming constant elasticity of scale equal to one). If there has been a gradual development towards more capital-intensive vessels, while Hicks-neutral technical progress has occurred over the same interval, the true isoquant will be like I_2. Seeking a point of tangency between a factor price line and the isoquants will obviously yield a higher optimal capital to labor ratio for the estimated I_1 than the true I_2.

Exactly the same thing could happen if the most able skippers replace their boats more quickly than others and sell their old boats to less able skippers. Then, given that there is a trend toward increased capital intensity of vessels, the more labor-intensive boats would be operated by the less able skippers, and so would appear to be less efficient than they really are.

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Appendix 1. Model Used for Drawing the Phase Diagrams in Fig. 2–7

The growth function is a modified version of the logistic function

$$G = b\left(\frac{W-a}{1-a}\right) + d\left(\frac{W-a}{1-a}\right)^2$$

where $b = 1$ and $d = -1$. The population level is expressed as a fraction of its natural equilibrium size ($G = 0$ when $W = 1$). Parameter a expresses the threshold value of viability ($G = 0$ when $W = a$; $G'_{W=a} > 0$). The condition for biological equilibrium is

$$G = AE^{\alpha}W^{\beta}$$

which, by substituting for G, makes it possible to find the biological equilibrium locus by solving for E as a function of W. The condition for economic equilibrium is

$$pAE^{\alpha-1}W^{\beta} = c$$

where p and c are determined by demand and marginal cost functions, as follows:

$p = hy^{-\delta}$

$c = (1 + sE)^{\gamma}$.

The following table shows the value of the parameters assigned when drawing the phase diagrams in the figures accompanying the text.

Figure	a	α	β	A	h	δ	s	γ
2	0	1	1	1	2	0	0	0
3	0.1	1	1	1	15	0	1	4
4	0.1	1	1	1	0.8	0.6	0	0
	0.1	1	1	1	0.0001	2	0	0
5	0.1	1	1	1	2	0	0.5	2
	0.1	1	0.25	1	2	0	0.5	2
6	0	1	0	1	2	0	0.5	2
7	0.1	1	1	1	10.5	0	0	0
	0.1	0.5	1	0.3	10.5	0	0	0

Appendix 2. Aggregating Effort in the Lofoten Fishery

On the assumption that crowding externalities are either not present at all or else affect all types of gear to the same extent, two equivalent units of fishing effort would be expected to yield the same catch when applied in the same area to the same fish stock. So, while the catch per unit effort may be different for the various types of fishing gear, a common measure of fishing effort is sought such that

$$y_{it}/E_{it} = y_{jt}/E^*_{jt}$$

where i and j denote different categories of fishing effort.

Defining a conversion factor a_{jt} as $E^*_{jt} = a_j E_{jt}$, we get $a_{jt} = (y_{jt}/E_{jt})/(y_{it}/E_{it})$. But over time there may be different rates of technological progress associated with different types of gear. Thus, if the rates of progress are γ_i and γ_j, respectively, a_{j0} and a_{jt} are related by $a_{jt} = a_{j0} \exp b_j t$ where $b_j = \gamma_j - \gamma_i$. This gives the following regression equation

$$\ln\left(\frac{y_{jt}/E_{jt}}{y_{it}/E_{it}}\right) = \ln a_{j0} + b_j t.$$

Coefficient b was found significant (at the 5% level) only for longline in terms of boat-weeks (with i representing gill net boat-weeks). In this case, b was 0.03215, which indicates that the efficiency of longline boats increased about 3% more annually than the efficiency of gill net boats. For the remaining cases, the conversion factor to be used was estimated when expressing all fishing effort in terms of gill net effort by the arithmetic mean of

$$\ln\left(\frac{y_{jt}/E_{jt}}{y_{it}/E_{it}}\right).$$

The table below shows the conversion factors used when expressing fishing effort in terms of gill net effort. The Danish seine and purse seine vessels were excluded from this analysis because of a shorter time series. Effort in these fisheries was converted to gill net effort by assuming that the same effort per unit of fish caught each year was necessary, in terms of gill nets, as in the gill net fishery itself. Total effort is given by

$$E_t = \sum_{i=1}^{a} E_{it} a_i e^{b_i t}.$$

	Man-weeks		Boat-weeks	
	a	b	a	b
Gill net	1.0	0	1.0	0
Longline	1.3570	0	0.6219	0.03215
Handline	0.5782	0	0.2179	0

Appendix 3. Data used in Estimating Frontier Functions

Data on output, capital, and labor were obtained from vessels sampled by the Norwegian Directorate of Fisheries for the purpose of assessing the profitability of the fleet. Only vessels larger than 40 ft (12.5 m) were sampled. Data on fish stocks were taken from reports of the 1980 meeting of the ICES (ICES 1980a, 1980b).

Output

Output is given as the gross value of landings. Since the length of the fishing season varies from a few to over 100 d at sea, it was necessary to define output in terms of per day at sea. The main reason for this discrepancy, despite the fact that only vessels used for the whole year were being sampled, is that a vessel may switch from one "fishery" to another (see below). All values have been converted to 1977 prices by means of price indices for cod and similar species published by the Norwegian Central Bureau of Statistics in *Økonomisk utsyn* in 1979.

Capital and Labor

Capital is recorded as the replacement value of the vessel hull, outfit (except fishing gear), and engine. These were converted to 1977 values by price indices published by the Norwegian Central Bureau of Statistics in *Monthly Bulletin of Statistics* and were summed. The indices used were as follows. Engine: prices of non-electric engines; electric and hydraulic outfit: prices of electrical engines etc.; vessel hull: prices of transportation equipment. Labor is recorded as the number of fishermen employed on each vessel.

Fish Stocks

The vessels considered exploit mainly two species, saithe (*Pollachius virens*) and cod (*Gadus morhua*). In addition, different vessel groups exploit different age groups of fish. This is determined partly by the area in which they fish and partly by the fishing gear used. Multiplying the number of fish in the relevant age group by the

TABLE A1. Results of estimating the translog function for the subsample of efficient vessels: $\ln y_t = \ln \alpha_0 + \lambda t + \alpha_L \ln L_{it} + \alpha_K \ln K_{it} + \alpha_W \ln W_t + \frac{1}{2}\gamma_{LL}(\ln L_{it})^2 + \frac{1}{2}\gamma_{KK}(\ln K_{it})^2 + \frac{1}{2}\gamma_{WW}(\ln W_t)^2 + \gamma_{LK}(\ln L_{it} \ln K_{it}) + \gamma_{LW}(\ln L_{it} \ln W_t) + \gamma_{KW}(\ln K_{it} \ln W_t)$. Data in parentheses are t-values. NI, not included (insignificant at the 25% level).

Fishery	λ	α_L	α_K	α_W	γ_{LL}	γ_{KK}	γ_{WW}	γ_{LK}	γ_{LW}	γ_{KW}	R^2	F
1	0.0180 (0.7)	2.1943 (4.0)	0.8241 (10.9)	0.6870 (2.3)	−0.7020 (2.0)	NI	NI	NI	NI	NI	0.79	94.4
2	−0.0432 (0.8)	8.7061 (3.5)	0.1787 (0.7)	1.7717 (3.1)	0.8440 (1.8)	NI	NI	NI	0.8809 (2.4)	NI	0.72	21.6
3	0.0088 (0.3)	2.0227 (1.5)	0.9606 (3.4)	0.8330 (6.8)	0.5294 (1.2)	NI	NI	−0.2336 (1.6)	NI	NI	0.81	74.3
4	0.0482 (1.8)	4.3799 (5.8)	4.5276 (3.7)	3.8995 (3.3)	0.6332 (1.6)	NI	NI	−0.6676 (3.7)	NI	−0.4733 (2.6)	0.87	51.3
5	0.0645 (0.5)	2.1043 (2.1)	1.5857 (1.9)	5.6336 (2.0)	NI	NI	NI	NI	−3.2521 (1.9)	NI	0.56	5.0

age-specific weight of fish gives the biomass of the exploited stock. This information is contained in ICES (1980a, 1980b).

Some idea of which age groups are predominantly exploited by each fishery can be obtained from ICES (1980a, 1980b) and various other sources, notably the Resource Surveys by the Marine Research Institute in Bergen. On the basis of this information regressions of the Cobb–Douglas function (14) were run for alternative compositions of stocks, retaining the ones that yielded the highest level of significance for parameter ν. The age groups included in each stock are listed in Table 2.

FISHERIES

A "fishery" is defined as a group of vessels exploiting the same fish stock, i.e. the same age groups of a certain species confined to but freely migrating within a given area. The information on this is not perfect, but for each vessel the following is recorded. (i) Species making up the bulk of the catch; for the purposes of this article the choice is between winter cod, spring cod, other cod (different age groups of *Gadus morhua*), and saithe. (ii) Area of operations, e.g. the Barents Sea, the Lofoten area, etc. (iii) Type of fishing gear used, e.g. bottom trawl, gill nets, etc. On the basis of this information, it was possible to distinguish between the six fisheries listed in Table 2. These cover most of the demersal fisheries in Northern Norway.

The data for each vessel are recorded for up to five "seasons." A change of season occurs as a consequence of a change in the mode of operations making it necessary to close the accounts and calculate crew shares. Each vessel may therefore participate in more than one fishery.

PERIOD CONSIDERED

Data used cover the period 1971–78, except for fisheries 2–5, where 1978 was omitted. The reason is that, beginning in 1978, those who compile the data abandoned the terms "spring cod" and "winter cod." The reason for retaining these terms in this article is that they refer to distinctly different age groups of cod.

Appendix 4. Translog Function and Separability of Fishing Effort and Biomass

A test of the hypothesis that the production function is separable in fishing effort and fish biomass is provided by estimating the parameters of a translog function (cf. Berndt and Christensen 1973). The translog function is not generally separable, but separability imposes certain restrictions on its parameters. The translog function can be written as (cf. Berndt and Christensen 1973)

$$\begin{aligned}\ln y = {} & \ln \alpha_0 + \alpha_A \ln A + \alpha_L \ln L + \alpha_K \ln K + \alpha_W \ln W \\ & + \tfrac{1}{2}\gamma_{AA}(\ln A)^2 + \tfrac{1}{2}\gamma_{LL}(\ln L)^2 + \tfrac{1}{2}\gamma_{KK}(\ln K)^2 \\ & + \tfrac{1}{2}\gamma_{WW}(\ln W)^2 + \gamma_{LK} \ln L \ln K + \gamma_{LW} \ln L \ln W \\ & + \gamma_{KW} \ln K \ln W + \gamma_{LA} \ln L \ln A + \gamma_{KA} \ln K \ln A \\ & + \gamma_{WA} \ln W \ln A.\end{aligned}$$

Assuming an exponential technological progress of the neutral variety gives

$$\alpha_A = 0,\ \gamma_{AA} = 0,\ \gamma_{LA} = 0,\ \gamma_{KA} = 0,\ \gamma_{WA} = 0,\ \ln A = \lambda t.$$

All variables are dated, but the time subscripts have been excluded. The marginal rate of substitution between capital and labor is

$$\mathrm{MRS}_{LK} = \frac{\partial y/\partial L}{\partial y/\partial K} = \frac{(\alpha_L + \gamma_{LL} \ln L + \gamma_{LK} \ln K + \gamma_{LW} \ln W)K}{(\alpha_K + \gamma_{KK} \ln K + \gamma_{LK} \ln L + \gamma_{KW} \ln W)L}.$$

Separability of fishing effort and fish biomass implies that MRS_{LK} be independent of W. This requires that γ_{LW} and γ_{KW} both be zero. Taking $(\partial/\partial W)\,\mathrm{MRS}_{LK}$ shows that this would also occur if

$$\alpha_K/\alpha_L = \gamma_{KW}/\gamma_{LW} = \gamma_{KK}/\gamma_{LK} = \gamma_{LK}/\gamma_{LL}.$$

Table A1 shows the result of estimating the parameters of the translog function under the above assumption of the nature of technological progress. For fisheries 1 and 3, which in general yielded the most satisfactory results, the values of γ_{LW} and γ_{KW} are not significantly different from zero, thus supporting the hypothesis of separability between biomass and fishing effort. For fisheries 2 and 4 one of these coefficients is different from zero at any reasonable level of significance, and for fishery 5, γ_{LW} is different from zero at the 5% level of significance. This is not consistent with separability between fishing effort and fish biomass. Since there is no reason to expect the technology to be different with respect to separability for any of these fisheries, these results are somewhat inconclusive. For fishery 6 all coefficients except α_L and α_K were insignificant at the 25% level.

The Cobb–Douglas function is a special case of functions separable in fishing effort and fish biomass obtained if γ_{LL}, γ_{KK}, γ_{WW}, and γ_{LK} are all zero. For fisheries 1 and 3, for which the separability hypothesis was most strongly supported, the critical significance level for coefficient γ_{LL} is 5 and 20%, respectively (two-tailed test), and for γ_{LK} it is 5% in fishery 3. The rest are insignificant. The validity of the Cobb–Douglas function thus can be questioned, although the evidence against it is not particularly strong.

NOTES

Cichlid Stocking and the Decline of the Galilee Saint Peter's Fish (*Sarotherodon galilaeus*) in Lake Kinneret, Israel

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GOPHEN, M., R. W. DRENNER, AND G. L. VINYARD. 1983. Cichlid stocking and the decline of the Galilee Saint Peter's fish (*Sarotherodon galilaeus*) in Lake Kinneret, Israel. Can. J. Fish. Aquat. Sci. 40: 983 – 986.

The catch of the Galilee Saint Peter's fish (*Sarotherodon galilaeus*), relative to the catch of nonstocked fish of Lake Kinneret, has declined since 1958 despite the intensive stocking of *S. galilaeus* fingerlings. The reduced relative *S. galilaeus* catch coincides with stocking of the Jordan Saint Peter's fish, *S. aureus*. Laboratory analyses of *S. galilaeus* and *S. aureus* feeding behavior and selectivities suggest that they may compete for zooplankton, a major food resource for both species. The decline of *S. galilaeus* means not only a relative reduction of the most valuable commercial species but also a disruption of the trophic dynamics of the lake. *Sarotherodon galilaeus* is the primary consumer of the dominant alga in the lake, the bloom-forming dinoflagellate, *Peridinium*, and thus is important in maintaining water quality. The impact of stocking practices on *S. galilaeus* suggests that fisheries policies must be integrated into the overall program of water quality management for Lake Kinneret and lakes in general.

GOPHEN, M., R. W. DRENNER, AND G. L. VINYARD. 1983. Cichlid stocking and the decline of the Galilee Saint Peter's fish (*Sarotherodon galilaeus*) in Lake Kinneret, Israel. Can. J. Fish. Aquat. Sci. 40: 983 – 986.

Les captures de Saint-Pierre de la mer de Galilée (*Sarotherodon galilaeus*) par rapport à celles de poissons non introduits dans le lac Kinneret déclinent depuis 1958, en dépit de peuplements intensifs de fingerlings de *S. galilaeus*. La diminution relative des prises de ce dernier coïncide avec l'ensemencement de Saint-Pierre du Jourdain, *S. aureus*. Des analyses en laboratoire du comportement et de la sélectivité alimentaires de *S. galilaeus* et *S. aureus* donnent à penser que les deux espèces peuvent être en compétition pour le zooplancton, une importante ressource alimentaire pour les deux espèces. Le déclin de *S. galilaeus* signifie non seulement une diminution relative de la plus importante espèce commerciale, mais aussi une perturbation de la dynamique trophique du lac. *Sarotherodon galilaeus* est le consommateur primaire de l'algue dominante du lac, le dinoflagellé à floraison, *Peridinium*, et remplit pour cela un rôle important dans le maintien de la qualité de l'eau. L'impact des pratiques de peuplement sur *S. galilaeus* laisse supposer que les politiques de pêche doivent être intégrées dans un programme global de gestion de la qualité de l'eau dans le lac Kinneret et les lacs en général.

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LAKE Kinneret, the only freshwater lake in Israel, currently supplies 30% of the country's freshwater and approximately 1800 t (100 kg/ha) of fish annually (Golani 1980). Thus, both water quality and fisheries production of Lake Kinneret are important national concerns. Since 1951 twelve exotic and two native fish species have been stocked into Lake Kinneret (Ben-Tuvia 1981) without adequate study of their impact on the native fish community which comprised 19 species including four endemics. Ben-Tuvia (1981) stated that stocking enhanced the total catch from this lake by approximately 400 t/yr. without negative impacts on the lake's ecology. Here we will show that increases in populations of stocked Jordan Saint Peter's fish (*Sarotherodon aureus*) are associated with relative suppression of the commercially most valuable native species, the Galilee Saint Peter's fish (*S. galilaeus*). We also present evidence for competition between *S. galilaeus* and *S. aureus*, and discuss the implications for the management of Lake Kinneret in particular and lakes in general.

Cichlid stocking and catch — To supplement the catch of *S. galilaeus*, stocking of Lake Kinneret began in 1951 with the planting of 240 000 *S. galilaeus* fingerlings (Fig. 1A). The number of *S. galilaeus* fingerlings stocked into the lake has increased, averaging 1.8 million (SD = 0.3) annually from 1971 to 1980. *Sarotherodon aureus* stocking began in 1958 and reached 3.9 million fingerlings by 1975 (Reich 1978).

The influence of stocking on the *Sarotherodon* catch is not clear (Pisanti 1978; Reich 1978). The *Sarotherodon* catch has increased at the same rate as that of nonstocked species such as the Kinneret sardine (*Mirogrex terraesanctae*) and other cyprinid species (Fig. 1B). We feel that like the cyprinids, increases in *Sarotherodon* catch are probably the results of changes in fishing gear and effort. In the late 1950s the increase in catch coincides with the change from cotton to nylon gill nets, the subsequent expansion of fishing hours from night to include daytime fishing and the introduction of purse seines (Reich 1978; Lake Kinneret Fishermen's Organization, personal communication). Access to new fishing areas in the northeast area of the lake following the "Six Day" war in 1967 also enhanced the fish catch from the lake. Increases in catch during the late 1970s correlate with increases in average boat size, increase in gill net sizes, the fishing of deeper waters and the beginning of sonar location of fish by about 30 smaller boats in addition to the purse seiners.

While a productive fishery for *S. galilaeus* existed before stocking, stocking is responsible for establishment of a fishery for *S. aureus*, which occurred only in low numbers in Lake Kinneret prior to 1958 (Ben-Tuvia 1978). We are concerned that the establishment of increased *S. aureus* populations in the lake may have suppressed the *S. galilaeus* population. Catch statistics of stocked fish in Lake Kinneret must be viewed relative to nonstocked fish to control for long term changes in fishing effort. We realize that different fish species such as *Mirogrex* and *Sarotherodon* are not captured with the same efficiency by the various fishing gears in use, but the catch of nonstocked fish can be used as a general indicator of changes in fishing effort. The appearance of *S. aureus* in the catch coincides with a decline of *S. galilaeus* catch relative to nonstocked species (Fig. 1C). Before *S. aureus* stocking

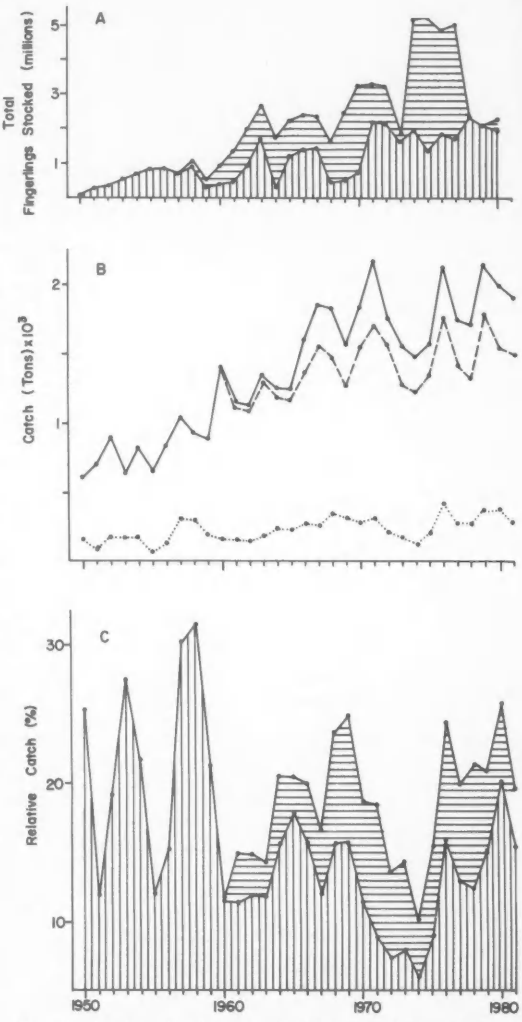

FIG. 1. *Sarotherodon* stocking and catch in Lake Kinneret during 1950–80: (A) Total stocked fingerlings (millions): ||||| *S. galilaeus*, ≡ *S. aureus*; (B) Commercial catch (tons): ●——● Total catch, ●– – –● Total catch of nonstocked fish, ●·····● Total catch of *S. galilaeus* and *S. aureus*; (C) *Sarotherodon* catch as a percentage of the catch of nonstocked fishes: ||||| *S. galilaeus*, ≡ *S. aureus*.

began, the average *S. galilaeus* catch was 21% (SD = 7.2) of the nonstocked catch. Since stocking of *S. aureus* the *S. galilaeus* catch has declined to 13% (SD = 3.6) of the nonstocked catch. This represents a 38% decline of the relative *S. galilaeus* catch compared to the catch of nonstocked fishes.

Feeding behavior and competition — Although we cannot

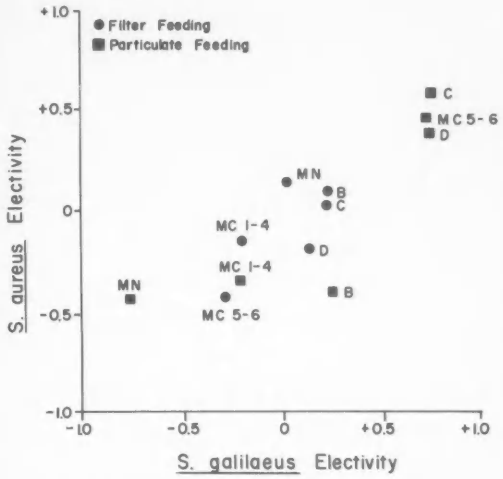

FIG. 2. *Sarotherodon galilaeus* / *S. aureus* indices of electivity of particulate (■) and filter (●) feeders (see text).

prove that competition between *S. galilaeus* and *S. aureus* caused the *S. galilaeus* decline, several facts suggest interspecific competition exists. *Sarotherodon galilaeus* and *S. aureus* apparently have a high degree of niche overlap. They are both mouth breeders and spawn during the same period. Generally, they are caught together by commercial fishermen, indicating substantial habitat overlap. Their diets also show much similarity throughout their lives. As fingerlings less than 5 cm total length, both species utilize zooplankton and benthic food items (particularly algae) (Gophen 1980; M. Gophen, unpublished data). As the fish mature, benthic foods become less significant and they become more dependent on plankton. The diets of adults of both species are dominated by zooplankton and phytoplankton throughout most of the year (Spataru 1976; Spataru and Zorn 1978). *Sarotherodon galilaeus* is particularly dependent on zooplankton during summer and fall when *Peridinium* resources are at their lowest (Pollingher and Berman 1978) but is reported to consume large quantities of *Peridinium* when it is available in winter and spring (Spataru 1976). Landau (1979) has suggested that the low condition factors and fat reserves of *S. galilaeus* during the summer are evidence for inadequate food conditions in the lake. *Sarotherodon aureus* also is most dependent on zooplankton in the summer and fall, and although it will consume *Peridinium*, it is reported to do so less intensively and to be less able to digest them (Spataru and Zorn 1976).

We have examined food competition using laboratory feeding trials to examine the feeding behaviors and selectivities of *S. galilaeus* and *S. aureus* for zooplankton prey (Drenner et al. 1982). Feeding trials consisted of adding fresh caught Lake Kinneret zooplankton to an aquarium and observing fish behavior. Laboratory studies show that the two species have similar behaviors when feeding on lake plankton. Both *Sarotherodon* species feed using three distinctive behaviors. They particulate-feed by visually locating and attacking individual prey, using an intense, directed suction for capture. They also filter-feed with a rapid series of nondirected suctions, drawing large volumes of water containing prey into the mouth. Similar filtering behavior is used to collect surface film-trapped prey, midwater suspended prey, and prey concentrated at the bottom. The third type of feeding behavior observed was a substrate scraping, utilized to remove prey from the surface of solid objects with the brushlike teeth on the lips. This behavior is probably used primarily to collect aufwuchs. Particulate feeding and filter feeding are both used to capture plankton.

Sarotherodon feeding behavior on zooplankton is dependent on fish size: *S. galilaeus* from 20 to 42 mm SL and *S. aureus* from 29 to 76 mm SL feed either as particulate feeders or as filter feeders depending on the sizes of available prey. For prey larger than 0.35 mm they feed as particulate feeders. *Sarotherodon galilaeus* and *S. aureus* larger than 62 and 76 mm SL, respectively, feed only as filter feeders.

Feeding selectivity was determined by monitoring aquarium zooplankton densities before and after short (< 1 h) feeding periods by groups of 1–10 fish (For methods see Drenner et al. 1982). Feeding selectivity was expressed as electivity (E) (Ivlev 1961). In general, both species have similar electivities for zooplankton prey (Fig. 2). When particulate feeding, electivity increases with prey size. The highest electivity values occur for *Ceriodaphnia*, *Diaphanosoma* and adult *Mesocyclops*, intermediate values for *Bosmina* and copepodites I–IV and the lowest values for nauplii. When either species feed as filter-feeders, their electivity values increase as a function of prey capture success (Drenner et al. 1982). Highest electivity values occur for *Ceriodaphnia* and *Bosmina*, intermediate values for *Diaphanosoma* and nauplii and the lowest values for *Mesocyclops* (C1–C4; and for C5 adults). These data show that *S. aureus* and *S. galilaeus* have similar feeding selectivities for zooplankton.

Discussion — It has been suggested that stocking of *S. aureus* into Lake Kinneret has increased the total commercial catch of the lake (Ben-Tuvia 1981). This implies that populations of stocked fish more efficiently channel energy into the commercial catch than do nonstocked fish. While this may be the case when introduced species occupy lower trophic levels than native species, it is unlikely that *S. aureus* increased energy flow into the commercial fishery. Our laboratory feeding trials show that *S. aureus* selectively utilizes the same zooplankton resources as *S. galilaeus*. Increased populations of *S. aureus* in the lake may simply reflect the subdivision of a finite zooplankton resource between *S. galilaeus* and *S. aureus* populations. This hypothesis is supported by the similarity in relative *Sarotherodon* catch before and after *S. aureus* stocking (Fig. 1C).

Displacement of *S. galilaeus* by *S. aureus* may have significant implications for water quality management of Lake Kinneret. *Sarotherodon galilaeus* is the most important native species consuming *Peridinium* (over 80% of average algal biomass for over 6 mo each year) (Serruya et al. 1979, 1980). While *S. aureus* ingests *Peridinium*, it does so less intensively (Spataru and Zorn 1978) and is less efficient at assimilating

Peridinium than *S. galilaeus*. Reduced grazing pressure on *Peridinium* from the displacement of *S. galilaeus* by *S. aureus* should result in increased *Peridinium* densities, increased dissolved organics and associated problems in water treatment for human and agricultural use. Since 1975, increases in total organic content of the lake have been reported (Serruya 1980; Gophen 1981, 1982).

We suggest that the most appropriate management strategy for Lake Kinneret is to increase the population of *S. galilaeus* by discontinuing *S. aureus* stocking. In addition to increasing grazing pressure on *Peridinium*, enhancement of the *S. galilaeus* population would be economically advantageous. *Sarotherodon galilaeus* is more valuable in the commercial market than *S. aureus*. Maintenance of a fishery for *S. aureus* is costly because *S. aureus* does not normally maintain abundant populations in the lake (Reich 1978; Ben-Tuvia 1978) and therefore requires continual stocking. *Sarotherodon galilaeus* may respond quickly to elimination of *S. aureus* stocking. Reduced stocking of *S. aureus* in 1978 and 1979 was associated with subsequent increases in the relative catch of *S. galilaeus* (Fig. 1C).

The stocking of fish without adequate understanding of their impact on the native fish community is not unique to Lake Kinneret. Although stocking of an exotic species may create a new fishery, it may not increase the yield of the fishery. When stocked fishes are close ecological analogs to the native species, they divert resources away from the native fish, potentially resulting in the stocked species displacing the native species. Because native species may be well adapted to the natural lake community, its displacement may disrupt community dynamics. It is time to recognize that the historic separation of the fields of limnology and fisheries biology is an artificial construct that does not reflect ecosystem function. Limnologists and fisheries biologists must begin to cooperate more effectively to achieve ecologically sound lake management.

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PERSPECTIVES

Homeostatic Characteristics of Single Species Fish Stocks in Arctic Lakes

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JOHNSON, L. 1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Can. J. Fish. Aquat. Sci. 40: 987–1024.

The results of investigations on the fish stocks of seven Arctic lakes covering a period of 23 yr are described. These lakes have remained largely undisturbed since their formation in late glacial times; all but one are completely autonomous and of comparatively small size. Such lakes provide a unique opportunity for the development and testing of conceptual models. In all cases the only fish species present is Arctic charr, *Salvelinus alpinus*. Length frequency distributions derived from gillnet catch curves are shown to be, within reasonable limits, representative of the actual populations in the lake, and not artifacts of the sampling procedure. Length frequency curves show a unimodal or bimodal distribution and this structure, in the absence of perturbation, appears to remain constant indefinitely. Individuals are of great age but age-at-length is highly variable. Age and size structure are shown to be comparable with the age and size structure of the dominant tree species in a climax forest; it is concluded that forces of great generality fashion these configurations. It is hypothesized that all species tend to move towards a state of least energy dissipation; this can be most readily seen in the dominant species at the climax in an autonomous system. The dominant species is characterized by large individual size, a high degree of uniformity, high total biomass, great mean age, indeterminate age-at-death, and a low incidence of replacement stock. After severe perturbation it is shown that the charr stock returns to a state of least dissipation without oscillation. Absence of oscillation during the return to the initial state, combined with the long-term stability shown in control lakes, indicates the presence of an effective damping mechanism; this in turn indicates the existence of organization within the stock as a whole. Organization develops through an interactive mechanism described under the doctrine of homeokinesis, which is responsible for energy equipartitioning and the maintenance of uniformity. These concepts help to explain phenomena observed in more complex systems and help our understanding of ecosystem functioning.

JOHNSON, L. 1983. Homeostatic characteristics of single species fish stocks in Arctic lakes. Can. J. Fish. Aquat. Sci. 40: 987–1024.

L'article qui suit contient les résultats de recherches, échelonnées sur une période de 23 ans, sur les stocks de poissons de sept lacs arctiques. Ces lacs n'ont pratiquement pas été dérangés depuis leur formation à la fin des périodes glaciaires; tous, sauf un, sont entièrement autonomes et de taille relativement petite. De tels lacs offrent une occasion unique d'élaborer et de vérifier des modèles conceptuels. Dans tous les cas, l'omble chevalier (*Salvelinus alpinus*) est la seule espèce présente. La distribution des fréquences de longueurs, établie à partir de courbes de capture de filets maillants est représentative, dans des limites raisonnables, des populations réelles qui habitent le lac et non le résultat d'artefacts dus aux méthodes d'échantillonnage. Les courbes de fréquence de longueurs montrent une distribution uni- ou bimodale et, en l'absence de perturbation, ce caractère semble demeurer tel quel indéfiniment. Les sujets sont très âgés, mais leur longueur à un âge donné est très variable. On constate que la composition par âge et par taille est comparable à celle de l'espèce d'arbre dominante dans une forêt au stade de climax; on en conclut que des forces universelles sont responsables de ces caractéristiques. Nous avançons l'hypothèse que toutes les espèces tendent vers un état de dissipation minimale d'énergie; ceci se manifeste le plus clairement chez l'espèce dominante d'un système autonome au stade de climax. L'espèce dominante est caractérisée par : une grande taille des individus, un haut degré d'uniformité, une abondante biomasse totale, un âge moyen avancé, un âge intermédiaire à la mort et une faible incidence

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de stock de remplacement. Après une forte perturbation, on constate que le stock d'ombles chevaliers retourne à un état de dissipation minimale sans oscillation. Cette absence d'oscillation pendant le retour à l'état initial, alliée à la stabilité à long terme démontrée dans les lacs témoins, indique la présence d'un mécanisme d'amortissement efficace; ceci à son tour est le signe de l'existence d'une organisation à l'intérieur du stock considéré comme un tout. Cette organisation se développe par le biais d'un mécanisme interactif décrit en termes d'homéocinèse responsable d'une équipartition de l'énergie et du maintien de l'uniformité. Ces concepts aident à expliquer les phénomènes observés dans des systèmes plus complexes et à mieux comprendre le fonctionnement des écosystèmes.

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APART from their great intrinsic interest, northern and Arctic lakes represent examples of ecosystems, now rare, that have been completely undisturbed by man since their formation. From the point of view of the investigator concerned with ecological mechanisms they have the further benefit of containing relatively simple biological systems that are, at the same time, almost completely autonomous or self-contained.

The advantage of working with such systems has been stressed by Holling (1973) who suggested that "theoretical models have generally not done very well in simultaneously incorporating realistic behavior of the processes involved, randomness and spatial heterogeneity and an adequate number of dimensions or state variables. If self-contained systems that were fairly homogeneous and in which climatic fluctuations were relatively small could be found ... they would reveal how the more realistic interaction of real world processing could modify ... patterns of systems behavior." Holling believes that systems approximating the theoretical conditions of a model are unlikely to be found, but if they do exist, then there is a good chance that they will be freshwater ones.

In actuality, it seems that there is a large number of lakes, closely approximating Holling's specifications, existing in the Arctic. Many of these lakes are quite small and homogeneous and capable of being manipulated without an inordinate amount of effort, and although climatic conditions in the Arctic tend to be highly variable, the lake environment appears to be reasonably well buffered.

In previous papers (Johnson 1972, 1973, 1975, 1976) I concluded that the fish stocks of northern lakes, mainly lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, and Arctic charr,[1] *S. alpinus*, exhibit length and age frequency distributions that are characteristic of the dominant tree species in a climax forest. Both fish and trees show a high degree of clustering around a modal size, as represented by length or stem diameter, in spite of a high variability in age and a growth pattern that is usually considered indeterminate. A general impression of stability and continuity is provided by the considerable size and age of the individuals and a notable feature is the low level of juvenile replacement stock.

If the structure of such widely differing ecosystems is similar, then there would appear to be principles in operation that are of considerable generality.

These results, and the conclusions derived from them, are not readily reconciled with accepted theory (Ricker 1975; Beverton and Holt 1957): growth rates are highly variable and difficult to express satisfactorily as a mathematical function; growth, in fact, appears to be size dependent and opportunistic rather than an ordered progression over time. The results also challenge the conclusions of the diversity–stability hypothesis (MacArthur 1955; Elton 1958) that simple systems tend to oscillate while complex ones tend towards stability. Although this thesis is at present in some disarray (Goodman 1975) it was at the height of its influence at the beginning of these investigations over 20 yr ago. It stimulated, to a considerable degree, the development of ideas that appear to be more conformable with observation, ideas that subsequently led to a general interpretation of ecological phenomena based on energy flow (Johnson 1981; L. Johnson, in preparation).

To account for the features observed in these undisturbed stocks I developed a model in which the steady state is density controlled by an interactional process, with juveniles being relegated to the periphery of the adult niche space and maintained there in a "stack." This stack is a group of relatively small-sized fish made up of individuals from various age groups. Individuals are allowed to move forward to join the established adult group when of the appropriate size and when opportunity occurs. During this transitional stage in their life history they grow rapidly, but on approaching the modal size of the establishment, growth slows down resulting in clustering around the modal value. The modal size represents a "best" integration of parameters determining energy inputs and outputs and is specific to the lake in question (Dutil 1982). Given self-regulation of the ultimate stock density and

[1]The name Arctic charr is used as a matter of personal consistency in preference to the single-r form, as recommended by the American Fisheries Society (1980). The form "charr" was adopted as the preferred spelling in the definitive work *Charrs: salmonid fishes of the genus Salvelinus* (Balon 1980) to which I was a contributor. The reason for the choice of the double-r form is explained in a preface to this work by W. H. Morton (p. 4–6). In this preface Morton points out that the AFS list itself recommended the double-r form in the 1948 edition. In England where the name originated, the double-r form was the accepted spelling until the late 1880s, although originally "charre." A personal rift between two eminent authorities, Francis Day and Albert Gunther, produced the cleavage, with Day and his influential protégée, C. Tate Regan, promoting the single-r form. "Char Lake" referred to later in the text is a statutory name not to be interfered with except by due process of law.

the fact that there is a most efficient, or most effective, size for each lake, the model merely implies that growth is size, not age, specific and that growth rates are higher over the length intervals where abundance is low and slowest where abundance is high. The model accounts for the continuous replacement of stock and the maintenance of constant density through accurate feedback control applied at the time of recruitment, the most sensitive point in the life cycle with respect to numerical control.

These results and their interpretation have been criticized on the grounds that the frequency distributions on which the model is based may be an artifact of the sampling procedure, as the data from which the distributions are derived were largely obtained from gillnet samples.

Fish growth is frequently considered to be a function of age although exhibiting considerable variation around the mean length at each age. Given the fact that a year class has greatest abundance at the time of hatching and is thereafter subjected to natural mortality in proportion to its abundance, an age-specific growth rate will result in a size distribution that follows, quite closely, age distribution, with large numbers of small fish and a logarithmically declining number in each increasing length interval. Fish samples taken from a population of which the true dimensions are unknown almost invariably show length frequencies that are bell shaped, approaching a Gaussian distribution. To meet the theoretical assumptions, such observed distributions are usually accounted for by (1) net selectivity, (2) differential recruitment (movement onto the fishing grounds from nursery areas over a range of sizes), (3) differential catchability (large fish are more readily caught than small ones), and (4) piling-up, a process first described by Baranov (1918) and subsequently discussed by Ricker (1975), Van Sickle (1977), and Power (1978). Piling-up, it is believed, results from a slowing down in growth rate as size and age increase so that, when combined with natural mortality, there is a tendency for more fish to enter one specific length interval than to leave it, either by growth or mortality.

That these various mechanisms do exist and play a part in shaping the configuration of the catch curves is not in question; the important feature is: are they sufficient, in themselves, to provide an adequate explanation of the observations? I believe that they are not because of three principal reasons. (1) Some lakes show extremely leptokurtic distributions in which over 70% of the total catch falls within a single 100-mm length interval (Johnson 1976); (2) within the modal length group there is very wide variation in age: frequently, representatives of all year classes taken in the establishment mode are encountered in this central length class (Johnson 1976, 1980); (3) the modal value of the same species varies greatly from lake to lake, although within lakes, the modal value remains constant over repeated sampling.

Power (1978) challenged the interactive model, maintaining that it is unnecessary; he suggested that control of population is through environmental constraints, although he conceded that lake trout numbers may be controlled by cannibalism. Power also believes that ages in northern fish stocks may be underestimated; this is undoubtedly a strong possibility, but it only affects the time scale, not the underlying mechanisms. Healey (1975, 1980), in a study of whitefish stocks in experimental lakes in the Yellowknife area, concluded that there is considerable evidence to support my findings with respect to stock structure but differs in his interpretation of the processes taking place. He suggested that when a stock is reduced by fishing there is an increase in growth rate until the stock recovers its original configuration. This possibility is, however, by no means excluded from the hypothetical model.

The postulated configuration and growth pattern demanded by the model has been confirmed by continuous and direct observations on anadromous Arctic charr over many years. The configuration of the sea-going stock of Arctic charr is strongly bimodal (Johnson 1980; Johnson and Campbell 1975), as determined by passage of the whole stock through a counting fence. Fish in the small mode (modal length 220 mm), when marked individually, showed a great increase in growth rate when they attained a length of 270–300 mm; thereafter, growth gradually declined as the modal length (600 mm) was approached (Johnson and Campbell 1976; L. Johnson, unpublished data). Further support for the hypothesis is provided by the extensive studies of Magnin (1977) on lakes in northern Quebec. After discussing the concept of gradual and continuous replacement of stock as in a climax forest, Magnin concluded: "Pour que la structure des populations de poissons des lacs nordiques se maintienne de la même façon, il faudra que plusieurs conditions soient réalisées: les poissons devront avoir une croissance moyenne faible avec de grandes variations individuelles, une maturité tardive, un taux de mortalité réduit et un faible recrutement. Toutes ces conditions semblent être réalisées chez la plupart des poissons nordiques et pas seulement chez les grands corégones et les touladis observés par Johnson (1973)."

Ultimately, the questions to be answered are (1) do samples taken in gillnets adequately represent the charr population in a lake as a whole and (2) does the population maintain itself in a steady state indefinitely? If these questions are answered in the affirmative then what are the underlying regulating mechanisms? To examine these questions a hypothesis has been established as follows. Provided environmental conditions remain within the normal range experienced over the recent past history of the lake, single species fish stocks in autonomous, or largely self-contained lakes, tend to assume a steady state characterized by high biomass accumulation, a high degree of uniformity in size irrespective of age, great mean age, and constant density. This steady state is maintained by internal homeostatic mechanisms resulting from intraspecific interaction. If the stock is displaced by an external perturbation it will return to the initial ground state when the perturbation is eliminated.

This hypothesis has been tested by investigations carried out on a number of Arctic lakes ranging over a wide latitude: from the northern continental coastline to the most northerly point of land in the Arctic Archipelago. Certain lakes were sampled at long time intervals; others have been subjected to intensive investigation annually over many years.

Description of the Lakes

All the lakes discussed have been essentially free from human interference since their formation in post-Pleistocene

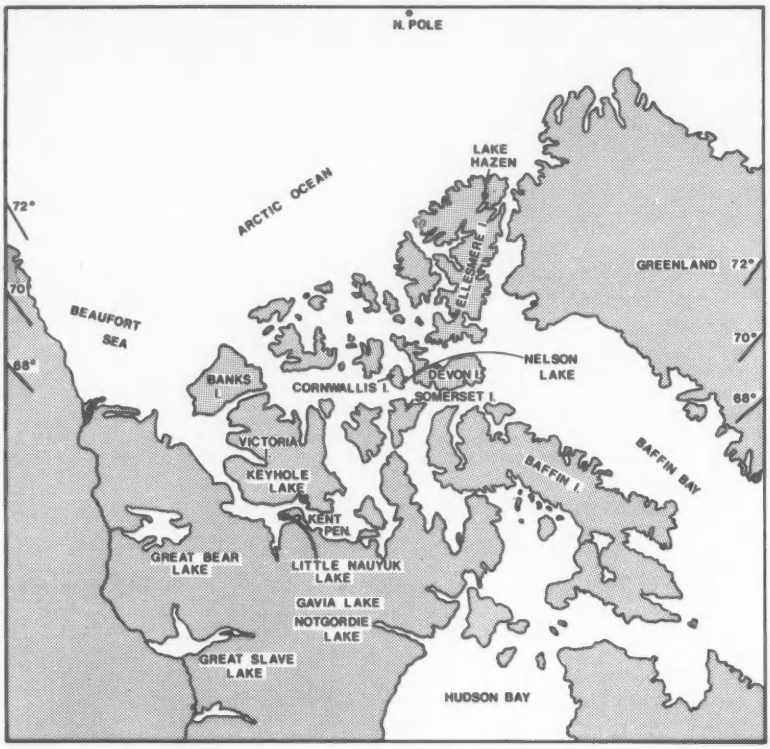

FIG. 1. Canadian Arctic showing location of the lakes investigated.

TABLE 1. Morphometric data on seven lakes in Arctic Canada from which samples of Arctic charr, *Salvelinus alpinus*, were obtained.

	Nelson (74°N, 92°15′W)	Keyhole (69°7′N, 106°14′W)	Little Nauyuk (68°22′N, 107°40′W)	Gavia (68°22′N, 107°40′W)	Notgordie (68°20′N, 107°35′W)	Hazen (81°50′N, 71°09′W)	Char (74°42′N, 94°53′W)
Area (ha)	60.2	48.6	44.6	17.4	7.1	54 200	52.6
Length (km)	1.10	1.047	2.108	0.62	0.66	74.0	0.95
Width (km)	0.515	0.710	0.417	0.521	0.179	7.0	0.76
Maximum depth (m)	11.0	6.5	15.0	8.0	6.0	(270)	27.5
Mean depth (m)	3.1	3.0	7.1	2.9	2.4	—	10.2
Volume ($m^3 \times 10^3$)	1842	1456	3167	505	170	—	5320
Winter volume ($m^3 \times 10^3$)	959	510	2139	230	66	—	4794
Winter ice thickness (m)	1.8	1.8	1.8	1.8	1.8	1.8–2.0	1.8
Ice as % of volume	47.9	65.0	32.4	54.4	61.2	—	17.8

times, some 6000–10 000 yr BP. The lakes range in latitude from Lake Hazen (81°50′N), in northern Ellesmere Island, to three small lakes on the Kent Peninsula on the northern continental coastline (68°22′N) (Fig. 1). All but one of the lakes are completely independent of any other water body so that their charr stocks are entirely "landlocked" or nonmigratory; only in Lake Hazen is there an anadromous charr population.

After spending 7–8 yr in freshwater following hatching, anadromous charr make their first migration to the sea at a length of 180–240 mm. They leave freshwater soon after breakup of the ice in spring and spend the summer feeding in the sea, returning to freshwater in the fall to overwinter. This pattern is repeated each year, except in years when adults may remain in freshwater to spawn.

The earliest study in this series was begun at Lake Hazen in 1958 by Ian McLaren, at that time a member of the Arctic Unit of the Fisheries Research Board of Canada (now the Arctic Biological Station (ABS) of the Department of

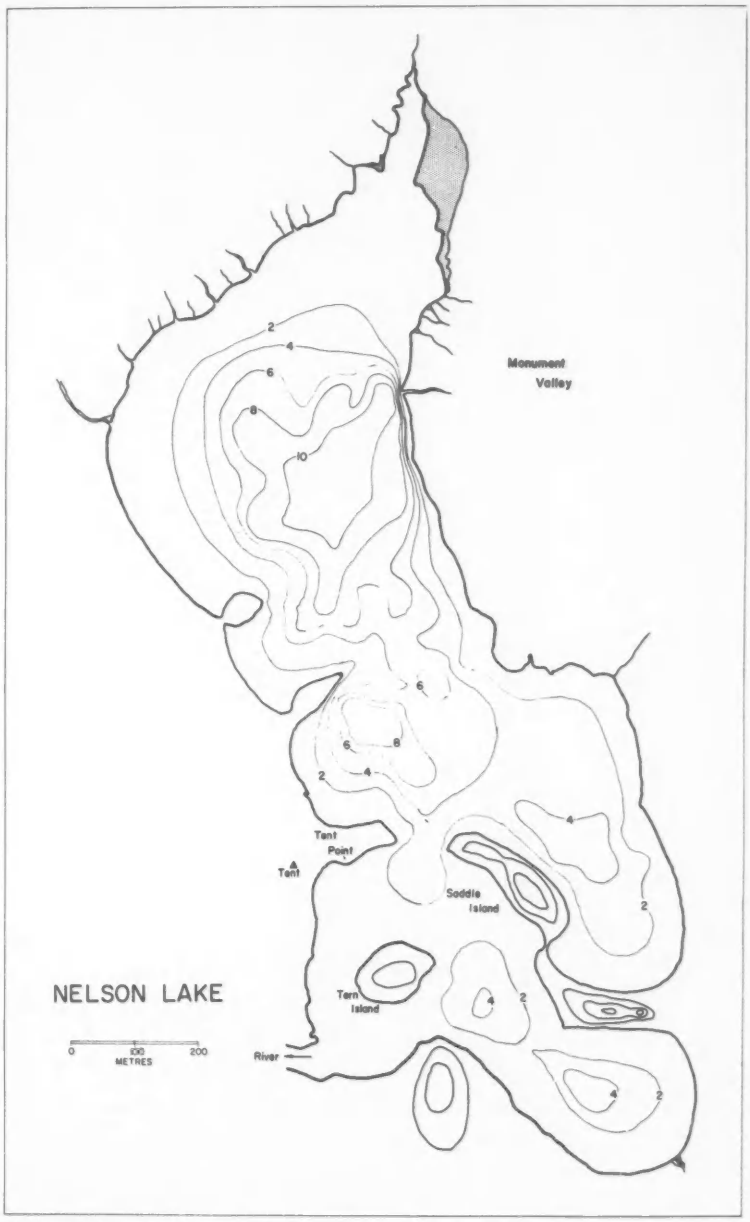

FIG. 2. Bathymetric map of Nelson Lake.

Fisheries and Oceans, Ste. Anne de Bellevue, Que.). A further sampling of Lake Hazen was carried out in August 1981 by a team from the Freshwater Institute (FWI), Winnipeg, Man., consisting of Michelle Roberge, Roger Peet, Robert Moshenko, and Allan Kristofferson.

In 1962, an extensive survey of the aquatic resources of the

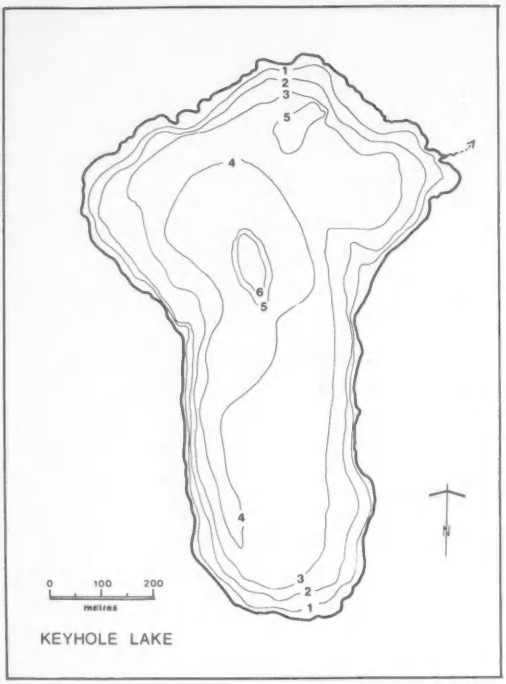

FIG. 3. Bathymetric map of Keyhole Lake.

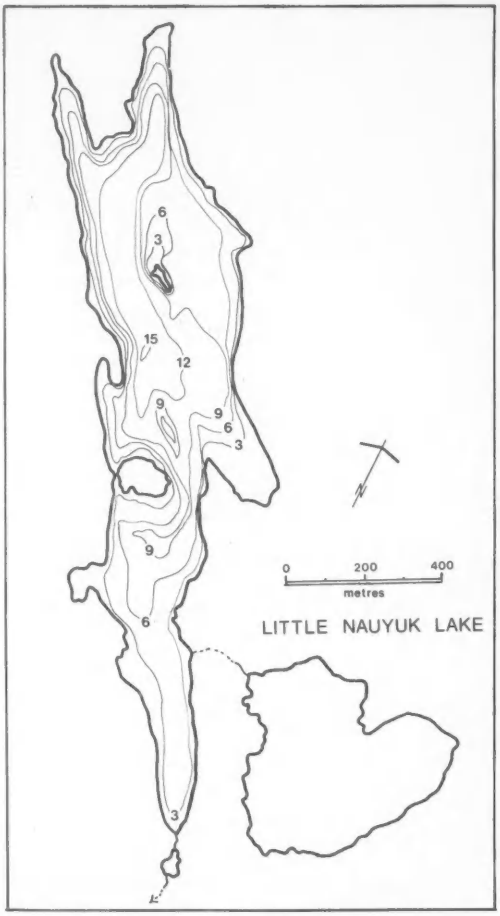

FIG. 4. Bathymetric map of Little Nauyuk Lake.

Arctic Archipelago was carried out by the staff of the Arctic Unit under the general supervision of Gerald Hunter. As part of this survey, studies on two small lakes were initiated, one on Nelson Lake, Cornwallis Island, and the other on Keyhole Lake, Victoria Island, 100 km west-northwest of Cambridge Bay. The study at Nelson Lake was conducted by Arthur Mansfield and Brian Beck and the work at Keyhole Lake was supervised by Gerald Hunter. Work on Keyhole Lake by the staff of the ABS continued until 1967 when it was terminated. Work there was resumed in 1975 when Scott Campbell and I of the FWI carried out a further series of investigations; we repeated this again in 1980. Also, in 1980 Bruce Stewart and Gary McDonald kindly agreed to resample Nelson Lake during the course of a land-use survey they were conducting in the general region. Nelson Lake was again sampled in 1982 by a crew from the FWI.

More continuous studies on Arctic charr were initiated in 1974 when I established a research station at Nauyuk Lake on the Kent Peninsula. This station was primarily devoted to studies of anadromous charr, but the existence of a number of small lakes in the vicinity, containing Arctic charr as the only fish species, provided an ideal opportunity to examine stock structure and its response to controlled exploitation on a long-term basis.

Lake Hazen (81°50′N; 71°09′W) (Table 1) is probably the most northerly large lake in the world. It is set in a long narrow trench 74 km long and 7 km wide, with a surface area of 542 km^2. The deepest recorded depth is 280 m. Discharge is via the Ruggles River that descends 155 m over a distance of 70 km, entering the sea in the Robeson Channel separating Ellesmere Island from Greenland.

Much of the water of Lake Hazen is turbid owing to the discharge of meltwater from neighboring glaciers. Frequently, ice does not clear from the surface in summer. In 1957, which was a comparatively early year, surface temperatures only reached 3°C (McLaren 1964). In the 2 yr in which charr sampling was carried out, 1958 and 1981, considerable ice remained all summer; in 1981, ice was beginning to reform during the period of sampling (13–18 August).

Nelson Lake (74°N; 92°15′W) (also called Twelve-mile Lake) (Fig. 2; Table 1), about 20 km E of Resolute Bay, Cornwallis Island, is one of a group of three that together form the Trafalgar Lakes. Nelson Lake and Hardy Lake both

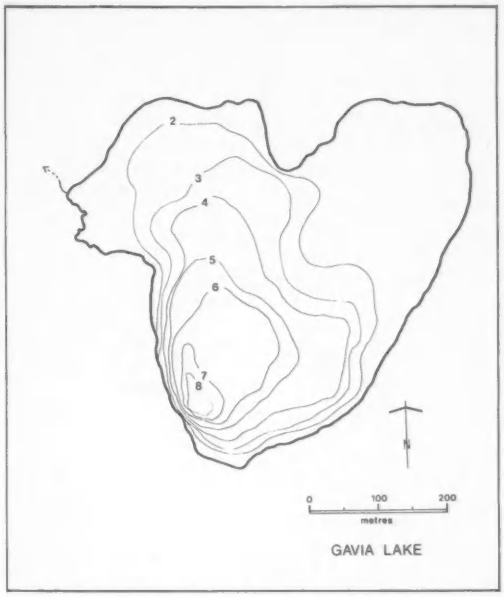

FIG. 5. Bathymetric map of Gavia Lake.

drain into Victory Lake, which in turn discharges to the sea at Assistance Bay via a short river, 4 km in length. Nelson Lake has a surface area of 60 ha and a maximum depth of 11 m. No charr have been observed migrating within the system or using the river as a migratory route, although occasionally, charr have been taken in Victory Lake having the appearance of being but recently returned from the sea (H. E. Welch, FWI, personal communication). None that might be considered sea run was taken during the extensive sampling in Nelson Lake in 1962, nor in the subsequent observations in 1980 or 1982.

Keyhole Lake (69°7′N; 106°14′W) (Fig. 3), just south of the outlet of Ferguson Lake on Victoria Island, is slightly smaller than Nelson Lake, having a surface area of 48.6 ha and a maximum depth of just over 6 m. It has a regular outline and very gradual contours.

Nauyuk Lake (68°22′N; 107°40′W), situated on the Kent Peninsula about 150 km WSW of Cambridge Bay, supports a robust population of anadromous charr. Three landlocked lakes in the vicinity were extensively investigated: Little Nauyuk Lake (Fig. 4), having an area of 44.6 ha and a maximum depth of 15 m, Gavia Lake (Fig. 5), 17.4 ha and a maximum depth of 8 m, and Notgordie Lake (Fig. 6), 7.1 ha in surface area with a maximum depth of 6 m.

Char Lake (74°42′N; 94°53′W) near Resolute Bay, Cornwallis Island, was intensively investigated between 1968 and 1973 as part of the Canadian International Biological Programme (PF Section) (Rigler 1975; Schindler et al. 1974). The lake has an area of 52.6 ha and a maximum depth of 27.5 m. The Arctic charr stock was investigated by MacCallum and Regier (1981). The charr stock was again sampled in 1982 by FWI personnel.

Apart from Lake Hazen, all the other lakes discussed are isolated from neighboring systems; the drainages are small and discrete and inflow is exclusively by surface seepage. Outflow is small and extremely low in the late summer and fall. Outlets either discharge directly to the sea (Little Nauyuk and Notgordie lakes), via other small lakes (Keyhole and Nelson lakes) or, in the case of Gavia Lake, as seepage down

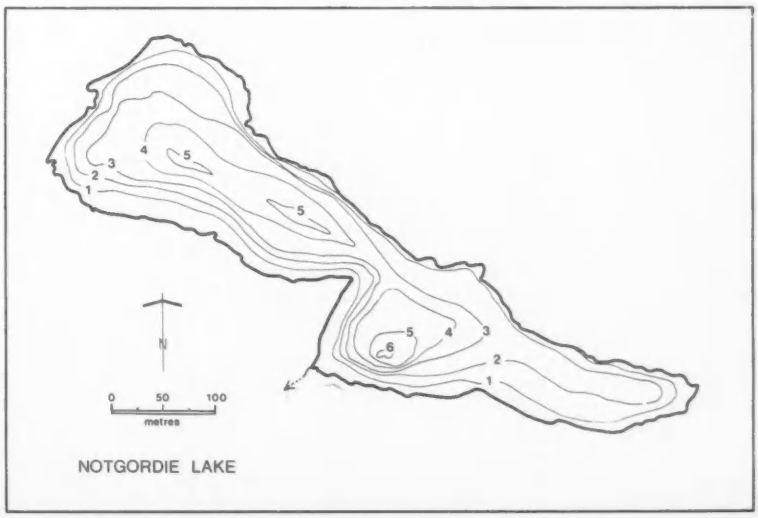

FIG. 6. Bathymetric map of Notgordie Lake.

a rocky hillside. In no case is there any doubt as to their completely landlocked status.

With the exception of Little Nauyuk Lake and to a lesser extent Notgordie Lake, the general configuration is that of a shallow depression in the surface till, probably initiated as a kettle during the retreat of the ice. Little Nauyuk is formed in a narrow trench between two sills of intrusive rock; in spite of this, the depth of the lake is not great, although the littoral region is very limited.

Primary productivity in Arctic freshwaters is very low, as shown in a detailed study of Char Lake (Kalff and Welch 1974; Welch and Kalff 1974). The total carbon assimilated amounts to about 20 g $C \cdot m^{-2} \cdot yr^{-1}$. Of this total only about 20% assimilated in the water column, the rest occurring on the lake bottom. As a result, the nature of the contours has an appreciable effect on primary productivity. Lakes with shelving contours such as Nelson, Keyhole, and Gavia are likely to be more productive than Little Nauyuk with its small littoral region.

All the lakes are ice covered for at least 9 mo of the year although the period during which they are ice free may vary from year to year, both in actual duration and as a result of the date of breakup. Over the 8-yr period of observation at Little Nauyuk Lake the earliest date that the lake became ice free was 7 July 1975 and the latest was 1 August 1978.

The late breakup means that a large fraction of the total available solar energy is utilized in melting ice, for it is not until at least 1 mo after the summer solstice that photosynthesis can take place without the light-filtering effect of ice cover.

Temperatures rise quite rapidly during the final stages of the icemelt; a band of relatively warm water (4–6°C) forms beneath the ice so that when open water finally occurs it is comparatively warm. Temperature thereafter rises quite rapidly; in the exceptionally early year of 1975 Little Nauyuk was isothermal at 10°C on 25 July and close to isothermal at 13°C on 21 August when maximum heat intake was reached. By 4 September temperatures had dropped to 8.8°C and ice cover regained by the end of that month. Normal maximum temperatures are between 7 and 9°C during the 3rd wk in August. In the more northerly Nelson Lake, temperatures seldom exceed 4–5°C and in Lake Hazen, 3°C is the maximum recorded. None of the lakes develop significant summer stratification.

Oxygen values remain close to saturation throughout the open water season. Under ice in June a deficit of 35–45% was observed in Keyhole Lake by Hunter (1970), but such low figures have not been obtained in the Nauyuk Lake group. No significant reduction in ice thickness (2–3 m) has occurred by the end of May, when investigations usually begin; the water at this time, even in the shallow Gavia Lake, is close to oxygen saturation. According to the work of Kalff and Welch (1974), photosynthesis in Arctic lakes begins as soon as the sun reappears above the horizon in late January or February, and it is just prior to this time that the lowest oxygen levels develop.

Faunistically, Lake Hazen is one of the most impoverished lakes in existence. In the plankton, there is but a single species of copepod, *Cyclops scutifer*, and two rotifers, *Keratella hiemalis* and *K. cochlearis*. Chironomids and water mites (*Hydracarina* spp.) are the only other invertebrates present (McLaren 1964). Arctic charr is the only resident vertebrate.

In Lake Hazen, as in many other lakes, there are two identifiable stocks of Arctic charr, one resident and the other anadromous. As with most migratory stocks, not all the adult charr go to sea in any given year (Johnson 1980); nonmigrants are usually the current year's spawning population. Stocks can usually be separated on the basis of growth rate, size, and color pattern in the adult stage but there are no detectable differences in juveniles.

In Nelson Lake the fauna is only slightly more varied; again, chironomid larvae and water mites make up the bulk of the charr diet, with the addition of small sphaerid clams, *Pisidium* sp., 2–3 mm in diameter. The other lakes show considerable differences in the macroinvertebrates present: in addition to the universal chironomid larvae and small clams there are several members of the so-called "marine-glacial relict" group, the large isopod, *Mesidotea entomon*, the amphipod, *Gammaracanthus aestuariorum*, and the opossum shrimp, *Mysis relicta* (Johnson 1964). In Little Nauyuk Lake all these three species occur. In Gavia Lake there is only *Mysis*, but in Notgordie not one of them is present; here, their place is taken by the amphipod *Gammarus lacustris*, which in turn does not occur in any of the other lakes considered.

In Char Lake in addition to chironomids, *Limnocalanus macrurus* and *M. relicta* are present.

These lakes exhibit the characteristics of a thermodynamically closed system throughout the period of ice cover: over this period there is no exchange of matter with the external world, only energy and entropy (Johnson 1981). Energy enters as sunlight and is dissipated in the form of heat. In summer, during the open-water season, some exchange of matter does occur with the emergence of, and egg-laying by, aquatic insects; in addition, there is a degree of predation on small charr by fishing birds, mostly loons (*Gavia* spp.) and gulls (*Larus* spp.). In spite of this activity the lakes probably approach more closely the closed, or autonomous, condition than do any other of the world's ecosystems, apart from certain Antarctic lakes that are permanently ice covered (Goldman 1970).

Methods

Sampling Gear

In all lakes the main sampling gear has been gill nets of multiple mesh size. In spite of their many possible disadvantages gill nets are a very effective gear in most lake situations; they have the advantages of low cost and easy transportation, are capable of being operated from a small boat with a low-powered motor, and are readily fished under the ice. Their disadvantage is that they tend to damage fish, if not in the capture then in their removal from the net; this makes them unsuitable for the capture of live fish for tagging or for stock estimates without population depletion. In small lakes this propensity to damage fish makes it impossible to carry out "preperturbation" sampling to determine the normal range of stock variability. Such estimates must therefore be made in control lakes with long intervals between sampling. Gill nets also raise questions of mesh selection and differential

catchability with respect to size.

In the early days of this program a standard gang for general usage consisted of six individual nets each 25 yd (23 m) long and 6 ft (1.8 m) deep. The mesh sizes used were: 1½ in. (38 mm), 2 in. (51 mm), 2½ in. (64 mm), 3½ in. (89 mm), 4½ in. (114 mm), and 5½ in. (140 mm) (stretched measure); up to 3½ in., the twine size used was 210/2 and above 3½ in. was 210/3. This gear, suitably modified to meet individual circumstances, was used regularly up until 1974.

In 1974 a survey type of gill net, manufactured by Lundgren's of Stockholm, Sweden, was designed to reproduce the original standard gang as closely as possible. This was constructed of very light materials and consisted of a single net, 100 m in length, made up of five panels, each 20 m long and 1.5 m deep. The individual panels were of the following mesh sizes (bar measure for metric usage; English units are stretched measure): 19 mm (1½ in.), 32 mm (2½ in.), 45 mm (3½ in.), 57 mm (4½ in.), and 60 mm (4¾ in.). A 30-m net of 10-mm (⅜ in.) mesh was added to improve the catching capacity for small fish. This gear was designated a 10-60 gill net.

In spite of these efforts we felt that improvements could be made; at all costs the gear had to be above suspicion of selectivity. Kipling (1957) showed that the best estimate of population characteristics can be made using multiple mesh sizes where each mesh size yields a catch whose length-frequency distribution overlaps those of its neighbors. To sample a fish population having a wide size range it is therefore desirable to have a net in which the mesh size increases geometrically.

In 1975 a second net was introduced (designated a 10-25 gill net) to meet, as closely as possible, the ideal of exponential increase of mesh size; this net had six 20-m panels of the following mesh sizes: 10, 12, 16, 19, 22, and 25 mm. The 10-60 net was modified to include an additional 20-m panel of 10-mm mesh; it therefore had the following mesh sizes: 10, 19, 33, 45, 55, and 60 mm.

When fished together (240 m of web = 1 unit of effort) these nets have proved to be a formidable sampling tool; in different lakes they have demonstrated a capacity to yield catch curves in which the modal length varied between 105 mm (Gavia Lake, 1975) and 750 mm (Namaycush Lake (Johnson 1976)). The lower limit of catchability with this gear is considered to be 100 mm although occasionally, smaller specimens are taken.

In addition to gill nets, beach seines, trap nets, hoop nets, and electrofishing equipment were used as appropriate. In the single instance of Notgordie Lake, fish poison (rotenone and Antimycin-A) was employed.

In Hazen Lake in 1958 standard gangs were fished and a total of 537 fish were caught. Beach seining netted a number of very small fish. In 1981 these sampling procedures were repeated, with the single difference that the 2-in. mesh was omitted from the standard gang; however, the total effort was supplemented with the addition of one gang each of 10-25 and 10-60 nets.

Sampling at Nelson Lake was begun on 29 June 1962 and continued until 5 August of the same year. The primary sampling gear consisted of standard gangs of nylon gill nets made up of web of the following mesh sizes: 12 mm (1 in.), 19 mm (1½ in.), 25 mm (2 in.), and 38 mm (3 in.). Each mesh size was represented by an individual net 46 m in length by 2 m deep. In the early part of the season, fishing was through the ice or along shore leads. The second and third samplings of Nelson Lake were carried out between 1–3 August 1980 and 2–6 August 1982 using 10-20 and 10-60 gill nets.

Keyhole Lake was initially sampled in 1962 and again in 1963, 1965, and 1967. The 1962 fishery was carried out using nylon gill nets with the following mesh sizes: 19 mm (1½ in.), 32 mm (2½ in.), and 45 mm (3½ in.); in 1963 and subsequent years these nets were supplemented with nets of 10-mm (⅜ in.) and 25-mm (2 in.) mesh; in 1965 and 1967 additional nets of 16 mm (1¼ in.) were employed. This lake was then resampled in 1975 and 1980, each time during the 1st wk in August, using identical gear on both occasions: four gangs of 10-25 and 10-60 gill nets. Electrofishing along the shoreline was carried out in 1975, but in 1980 the equipment failed on the eve of departure for the lake, so the exercise could not be repeated.

Little Nauyuk and Gavia lakes were sampled briefly in 1974 using the original 10-60 net; in all subsequent years both 10-60 and 10-25 gill nets were fished simultaneously. Both lakes were intensively fished along the shoreline using electrofishing gear. In Little Nauyuk Lake, trap nets and hoop nets were used extensively in 1978. In Notgordie Lake all available methods were used, including rotenone and Antimycin-A, to obtain as large a sample as possible over the shortest time period.

In Char Lake a variety of gear was employed between 1969 and 1972 (MacCallum and Regier 1981). Trap nets (Beamish 1972) and angling were employed most extensively, capturing 5800 and 4000 charr, respectively. In 1982 only 10-25 and 10-60 gill nets were used and a sample of 274 charr was obtained.

All fish captured were individually weighed to the nearest gram, or nearest 10 g, depending on size. Fork length was measured to the nearest millimetre. In Little Nauyuk Lake, during the intensive fishery of 1975, all fish were measured but only 20% were weighed individually.

Aging Techniques

Saggital otoliths were removed for age determination and then stored dry in individual envelopes for later reading in the laboratory. Otoliths were read under a binocular microscope after clearing in a 2:1 solution of benzyl benzoate and methyl salicylate.

Two schools of thought tend to complicate otolith interpretation. Grainger (1953) concluded that a check mark in the nuclear region represented the end of the first summer band, but Nordeng (1961) believed that this check is laid down in the middle of the first summer after hatching. Field collection of newly hatched and slightly older charr tends to confirm Nordeng's interpretation. Ages read by personnel at ABS thus tend to be 1 yr greater than those read at the FWI. Otoliths from Lake Hazen in 1958, Keyhole in 1962–67, and Nelson Lake in 1962 were read at ABS; all others were read at the FWI. The material from Lake Hazen in 1981 was, however, read according to Grainger's interpretation. To minimize confusion, all ages have been adjusted to conform to Nordeng's interpretation.

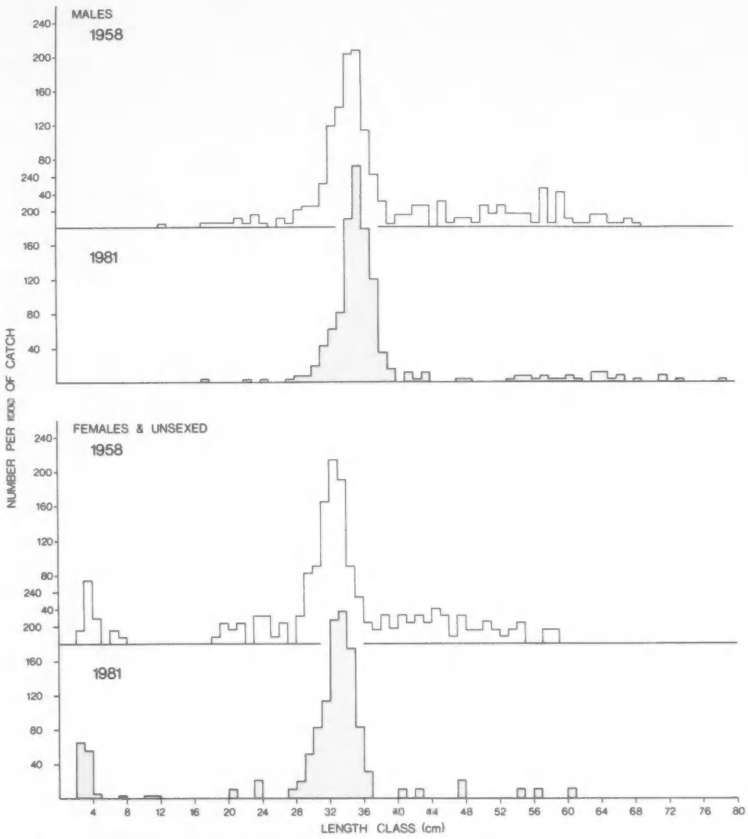

FIG. 7. Catch histogram of the length distribution of male and female and unsexed Arctic charr, *Salvelinus alpinus*, from Lake Hazen. The unsexed specimens comprise the modal group in the 34- to 40-mm length range.

CONDITION

The absolute condition factor (Hile 1936; Le Cren 1951) is used as a comparative index of "fatness." This relates the weight of a specific fish to the weight of an idealized fish of the same length growing isometrically. The value of the index for the isometric fish is always 1 so that condition is measured by departure from unity. It is ideal for the comparison of changes in the weight of fish of modal length either within or between years provided the modal length remains constant. If fish of different lengths are compared, then distortions occur. The absolute condition factor (K) is given by

$$K = \frac{W \times 10^5}{L^3}$$

where W is the weight in grams and L is the length in millimetres.

PHYSICAL LIMNOLOGY

In addition to the observations and measurements on the catch, routine measurements of oxygen and temperature were made in Little Nauyuk and Gavia lakes. A modified Winkler method was used for oxygen determination (American Public Health Association 1976) and an electrical resistance thermometer was used for measuring temperature.

FISHING REGIMES

Hazen and Nelson lakes were designated control lakes and were only sampled on an intermittent basis, as opportunity occurred. In Keyhole Lake the charr stock was severely reduced during the period 1962–65 by an intensive fishing program (Hunter 1970). It was then allowed to remain fallow for 10 yr until resampled in 1975; the most recent sample was taken in 1980.

TABLE 2. Stock characteristics of Arctic charr, *Salvelinus alpinus*, from Lake Hazen in 1958 and 1981.

	No.	Mean length (mm)	Mean weight (g)	Mean age (yr)	Modal length (mm)	Condition factor (K)	Catch per unit effort (No.)
>270–<400 mm							
1958							
Males	211	340	339	18.7	355	0.7915	93
Females	140	327	320	17.0	325	0.8040	
1981							
Males	262	347	403	18.3	355	0.9201	100
Females	96	329	335	16.8	335	0.9214	
>400 mm							
1958							
Males	91	532	1135	21.6	—	0.7538	
Females	42	475	900	20.8	—	0.8398	
1981							
Males	36	579	2003	21.3	—	1.0320	
Females	7	499	1039	21.3	—	0.8362	

Little Nauyuk was heavily fished in the 1st year to remove between one-third and one-quarter of the total estimated stock. Two annual fisheries were subsequently imposed on the lake, one immediately after ice-out and the other as late in the fall as could be arranged, usually in late August or early September. The total annual harvest of 500–600 fish ($12–15 \cdot ha^{-1}$) was divided evenly between the two fisheries. This regime was designed to provide information on density changes over the summer season, changes in feeding habits, growth rates, movement, and distributional patterns. The fall fishery had to be abandoned in 1980 and 1981 because of short field seasons.

The effort in Gavia Lake was concentrated in the period immediately following breakup, with a single fishery maintained at a constant level of about 400 fish annually.

In Notgordie Lake the aim was to impose a massive fishery on the lake over a minimum period of time, using all available methods, to obtain the best instantaneous assessment of the stock.

Results

LAKE HAZEN

The Arctic charr stocks of Lake Hazen remained virtually unchanged over the 23 yr between the samplings. In spite of its large size and the relatively low sampling effort, both length and age frequency distributions show no change over the years. In both sexes there are three readily identifiable length groups (Fig. 7; Table 2), two with bell-shaped distributions and a third group that is quite uniformly represented.

The smallest group (mean length 30 mm), composed mainly of 0+ and 1+ year classes, was taken in considerable numbers by beach seining. Even the smallest fish in this group (21 mm) had absorbed its yolk sac, a process not normally completed until a length of about 30 mm has been reached; this implies small eggs and a very small size at hatching. Very few charr between 40 and 200 mm in length were collected in either year.

The most abundant group has a modal length of 330–340 mm; as in most charr systems the males are slightly larger than the females. Males are also more abundantly represented in the sample in both years: in 1958 the sex ratio is 1.66:1 in favor of males, and in 1981, the ratio is 2.9:1. In both large and small groups the condition factor is higher in 1981 than in 1958. This difference may be due to the observations being made in mid-August in 1981 compared with 1958, when observations started in July and terminated in early August. Perhaps surprisingly, condition factors in both years are high considering the northern latitude of the lake.

The largest group in Lake Hazen is unusual in that it does not show any tendency to cluster; a range of sizes appears to be uniformly represented. This configuration is repeated with a high degree of similarity in both years, the main difference being higher relative abundance in 1958. The age distribution for both intermediate and large groups shows a great deal of overlapping, indicating much higher growth rates in the larger group (>400 mm) (Fig. 8).

There appear to be three possible reasons for this distribution. The first is that the larger group represents a portion of the anadromous stock that has not gone to sea in the year of sampling. This is not uncommon in anadromous charr stocks (Johnson 1980) but it is usually the current year's spawners that remain behind. Second, many of the large group in Lake Hazen do not appear to be spawning in the current year; it is therefore possible that the return run from the ocean has already begun. The third possibility is that some of the large fish have adopted a cannibalistic habit and have been able to increase their growth rate without necessarily going to sea.

The greater relative number of large charr in 1958 may be accounted for by sampling at the mouth of "Section" Creek, the only nonturbid stream on the north side of the lake. I. A. McLaren (unpublished data) found that it was only in the vicinity of the mouth of this stream that prespawning, maturing charr were encountered. In 1981 this region could not be fished because of ice conditions and very few spawners for the current year were captured.

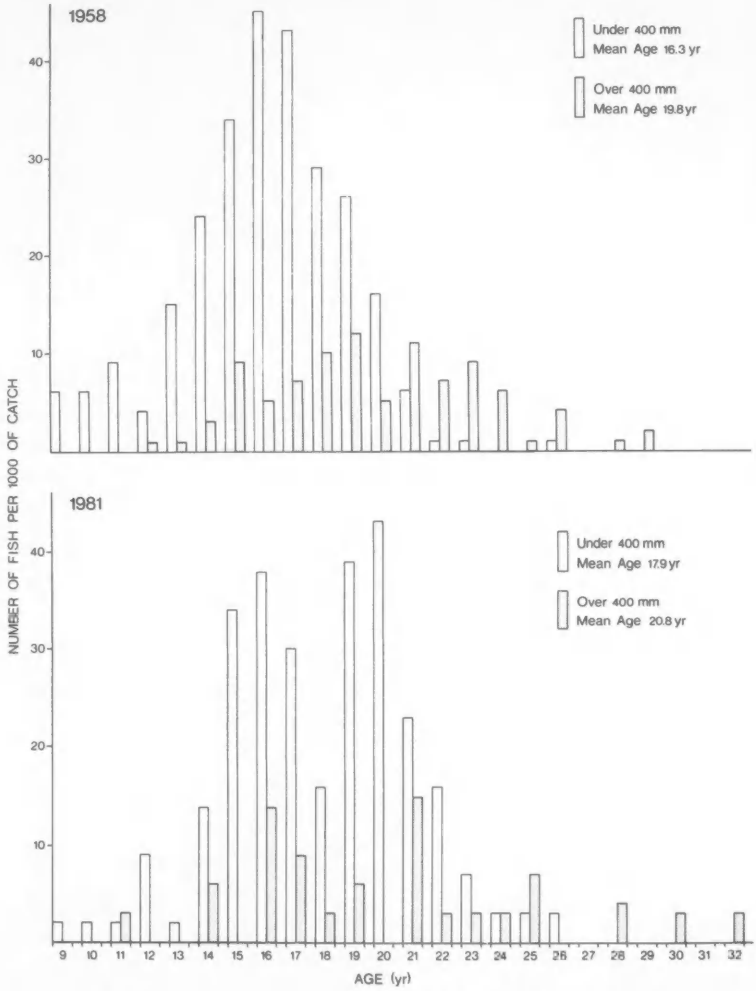

FIG. 8. Age distribution of Arctic charr, *Salvelinus alpinus*, in Lake Hazen in 1958 and 1981. The population has been arbitrarily divided into fish under 400 mm and fish over 400 mm. Thre is a great deal of overlapping in age between the groups, indicating great differences in growth rate.

Density as measured by catch per unit effort shows no appreciable difference between the years. McLaren gives a figure of 93 charr captured per lift of the standard gang. In 1981 the comparable figure was 84 fish, which, when adjusted to compensate for the lack of the 2-in. mesh-net, gives a figure of approximately 100 fish per gang.

NELSON LAKE

Between 29 June and 5 August 1962 a total of 838 Arctic charr were removed from Nelson Lake. This is equivalent to 14 fish (mean wt = 321 $g \cdot ha^{-1}$) or 4.5 $kg \cdot ha^{-1}$.

The length frequency of the catch shows strong bimodality with modes at 195 and 345 mm. Within each mode the stock is remarkably uniform in size. In the large mode (fish > 270 mm) 82% fall within 25 mm on either side of the modal value (Fig. 9; Table 3).

The effect of mesh selection on these results is of interest (Fig. 10). The smallest mesh size, 1 in. (12 mm), catches mostly charr in the small mode (180–240 mm) although a few larger charr are also taken. The 1½-in. (19 mm) mesh catches a few fish in the smaller mode but they mostly fall

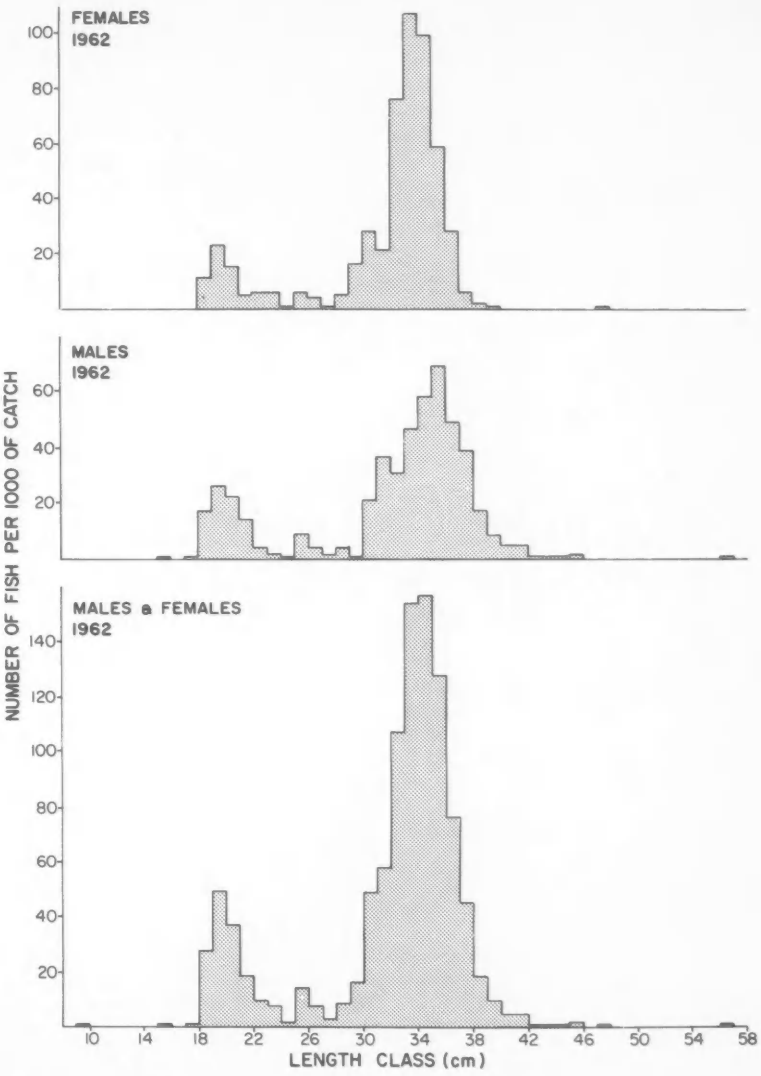

FIG. 9. Histogram showing length distribution of Arctic charr, *Salvelinus alpinus*, in Nelson Lake in 1962.

within the larger mode; the 2-in. (25 mm) catches no small fish but yields a distribution identical with that of the larger mode in the previous mesh size; in the 3-in. (38 mm) net there is only a very small catch but it all lies within the limits of the catch of the 2-in. mesh. Between the 1½-, 2-, and 3-in. mesh sizes there is no sign of a shift in length frequency distribution.

The charr of Nelson Lake in the pristine state are old (Fig. 11) but apparently not quite so old as those of Lake Hazen. The mean age of fish in the smaller mode (modal value 195 mm) is 9.5 yr with a range from 6 to 14 yr. The mean age of the larger group is 16 yr but the variation in age at modal length is great, showing a range of values from 7 to 24 yr. The age of fish in both modal length groups spans all ages encountered within the "bell" as a whole.

The significance of the small mode is not immediately

TABLE 3. Stock characteristics of Arctic charr, *Salvelinus alpinus*, from Nelson Lake for the years 1962, 1980, and 1982.

	Sample size	Mean length (mm)	Mean weight (g)	Mean age (yr)	Modal length (mm)	Mean weight at mode (g)	Mean age at mode (yr)	Age range at mode (yr)	Max. length	Condition factor (K)
1962										
Males	409	349	335	16.3	355	331	16.1	12–21	565	0.7444
Females	430	338	321	14.2	345	313	15.7	11–24	475	0.8326
Combined	839	343	328	15.1	345	321	15.9	11–24		0.7818
1980										
Males	46	363	491	14.6	345	332	13.9	11–18	540	0.8085
Females	51	344	344	13.8	345	336	14.1	11–19	410	0.8183
Combined	97	353	412	14.2	345	334	14.0	11–19		0.8134
1982										
Males	22	345	427	14.3	315	277	13.6	12–16	570	0.8860
Females	37	340	342	14.6	335	332	13.3	12–15	390	0.8830
Combined	59	342	374	14.5	325	307	12.8	12–14		0.8950

apparent. Superficially it might appear to be a juvenile "stack" although the fish are old for such a situation. Considering that 7% of the females and 10% of the males in this group are in prespawning condition, it seems to exist in its own right. In the larger mode 23% of females and 27% of males were ripening gonads in 1962. Lakes in which two recognizable groups of charr exist together are quite common (Johnson 1980), but the status of such groups, whether they represent species, subspecies, incipient species, or are merely the reflection of ecological conditions, is a matter of contention among charr biologists (Nordeng 1981; Nyman 1981).

Resampling Nelson Lake in 1980 and 1982 showed that considerable reduction in stock density had occurred. This is apparently the result of fairly intensive exploitation by the Inuit of Resolute Bay. In spite of this reduction in density the general characteristics of the age and length structure remain intact. There is still a well-defined mode at 345 mm in 1980 but this had declined slightly to 325 mm in 1982 (Fig. 11; Table 3). In both 1980 and 1982 the age distribution within the modal length group is quite comparable with that in 1962, although the more extreme values at each end of the distribution have been eliminated. Only 54% of the gillnet catch over 270 mm, in both 1980 and 1982, falls within the central 50-mm length class. In 1980 the smaller mode showing in the 1962 catch does not appear, probably because of the location of the nets. Most of the fish in the smaller mode in 1962 were taken in the northwest portion of the lake, and in 1982 they were again located in this region. As in 1962, 10% of the females and 27% of the males in this smaller group were found to be in prespawning condition. In 1982 a third mode (modal length 65 mm) was obtained by electrofishing the shorelines.

Apart from the absence of the smaller mode in 1980, the observed differences in the catches are very small. In 1962 and 1980 the modal length is 345 mm; in 1982 it is somewhat less well defined but lies between 335 and 345 mm. Similarly, the modal value for the small mode is somewhat less in 1982 than it was in 1962. The mean weight of fish in the modal group was 321 g in 1962, 334 g in 1980, and 307 g in 1982. The mean age of the modal length class was 15.2 yr in 1962, 14 yr in 1980, and 13.8 yr in 1982. Within each length class there is a great deal of variation in the age distribution; 16+ and 17+ are the most frequent year classes in the modal group in 1962, 13- and 14-yr-olds in 1980, and 12-, 13-, and 14-yr-olds in 1982. Mean ages tend to remain constant but the age composition of the length classes changes with time.

Attempts to compare stock density proved difficult owing to a change in gear type between 1962 and 1980, but there has undoubtedly been a considerable decline over the years. The best estimate of catch per unit effort of charr of over 270 mm in length in 1962 is 60 charr per 240-m net, 34 charr per 240-m net in 1980, and only 28 charr per 240-m net in 1982.

KEYHOLE LAKE

Sampling began in Keyhole Lake (48.6 ha) in 1962 with the removal of 860 charr; in 1963 a further 4154 were removed, and in 1965 another 2128. In 1967 only 86 fish were captured. This represents a total harvest, by gillnetting, of 7228 Arctic charr, equivalent to 149 fish·ha^{-1}. This is a significant fraction of the initial standing stock estimated at 7900 charr aged 7 yr and older (Hunter 1970). In terms of the surface area the initial standing stock is estimated at 163 charr·ha^{-1} having a weight of 43.8 kg·ha^{-1} (Table 4).

In 1975 and 1980 the lake was revisited; samples of 386 charr (7.9·ha^{-1} or 1.86 kg·ha^{-1}) and 730 charr (15·ha^{-1} or 5.5 kg·ha^{-1}) were obtained, respectively.

The samples in 1962 and 1963 gave rise to slightly skewed unimodal catch curves with modal length values of 295 and 310 mm, respectively; age modes were at 8 and 9 yr, respectively (Fig. 12). In 1965 the distributional pattern changed significantly, showing a strong tendency to bimodality in both length and age. Apparently the remnants of the original establishment have increased in size giving rise to a mode at 345 mm with a corresponding mode for age at 11 yr. At the same time, there has been a considerable upsurge of juveniles to replace the charr removed; these juveniles now form a

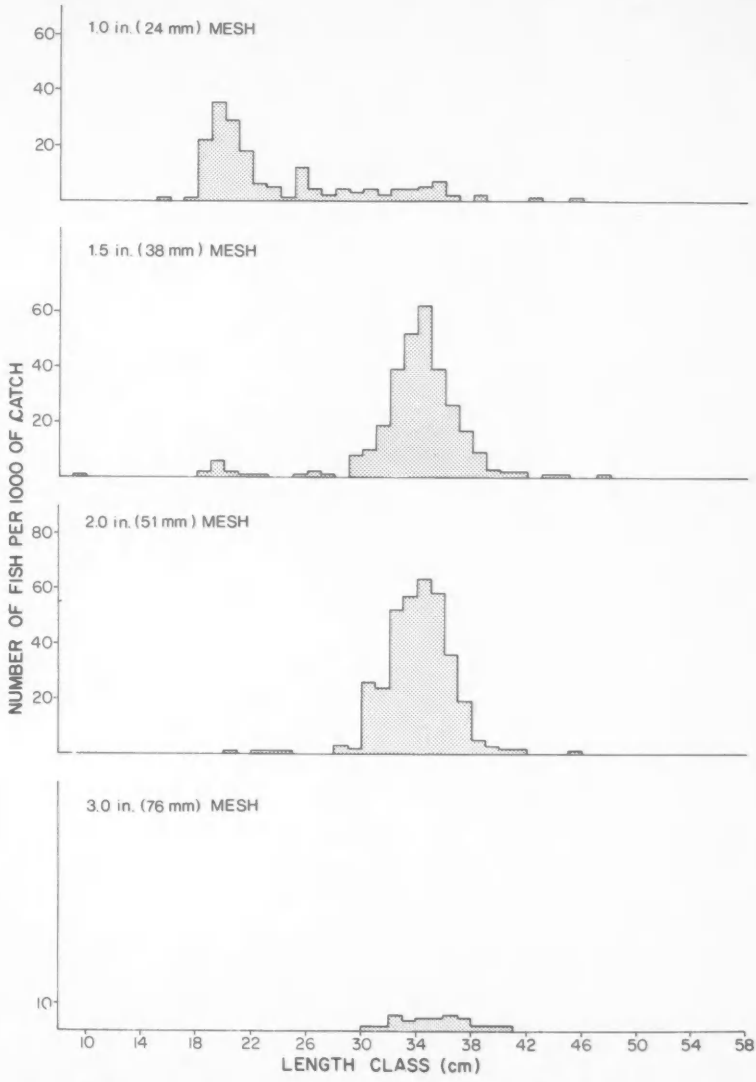
1.0 in. (24 mm) MESH
1.5 in. (38 mm) MESH
2.0 in. (51 mm) MESH
3.0 in. (76 mm) MESH
NUMBER OF FISH PER 1000 OF CATCH
LENGTH CLASS (cm)
10 14 18 22 26 30 34 38 42 46 50 54 58

FIG. 10. Histogram of the length distribution of Arctic charr, *Salvelinus alpinus*, in Nelson Lake showing the effect of mesh selection.

mode at 220 mm. A modal age of 5 yr indicates that the majority of this 220-mm modal group were in the lake at the start of the experiment 3 yr previously.

By 1975 the stock configuration has reverted to a state very similar to that of 1962, although the shoulders of the curve are broader and there is a uniquely high concentration of charr in the modal length class. The mean age at modal length (314 mm) is now 10 yr, an apparent increase of 2 yr over the 1962 value of 8 yr. The mean weight of an individual fish is identical, in 1975, to that recorded in 1962.

In 1975, electrofishing along the shoreline demonstrated the existence of a mode of smaller sized fish, with a maximum length frequency at 115 mm. Within this mode there is a considerable range of age, individuals varying between 3 and

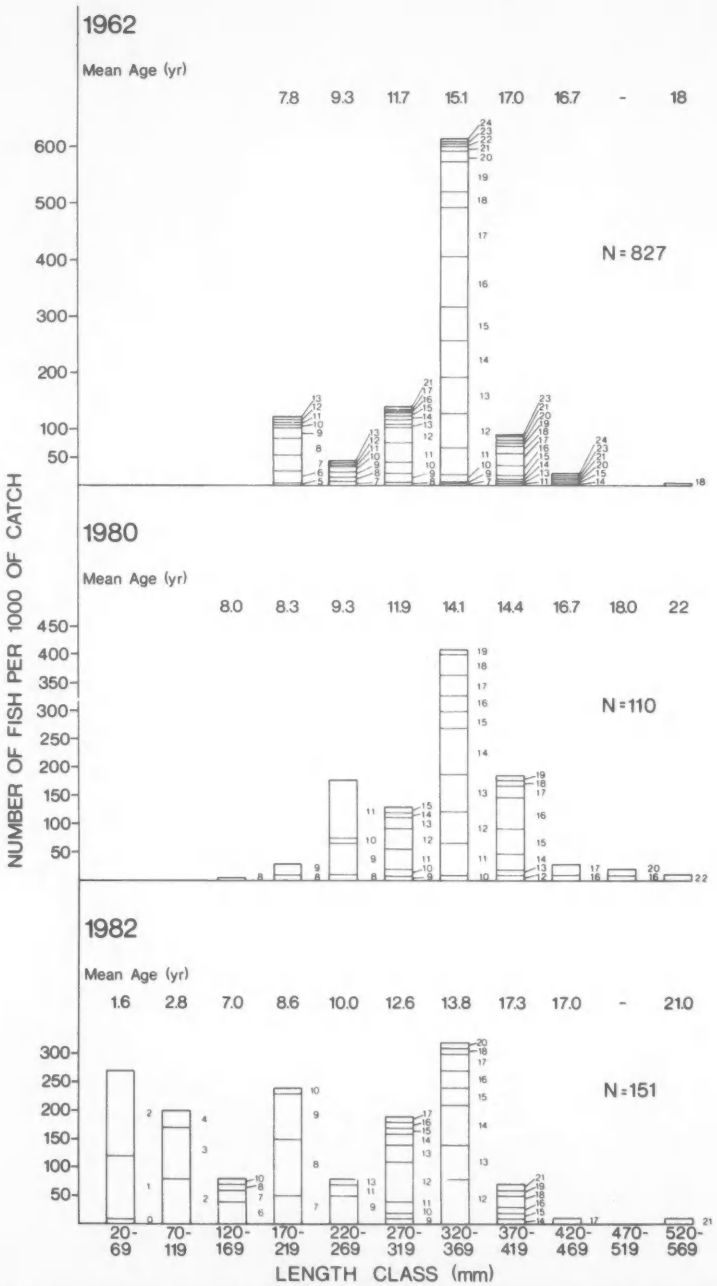

FIG. 11. Histograms of length and age distribution of Arctic charr, *Salvelinus alpinus*, in Nelson Lake in 1962, 1980, and 1982. Age and modal values remain remarkably constant but density has declined markedly in recent years.

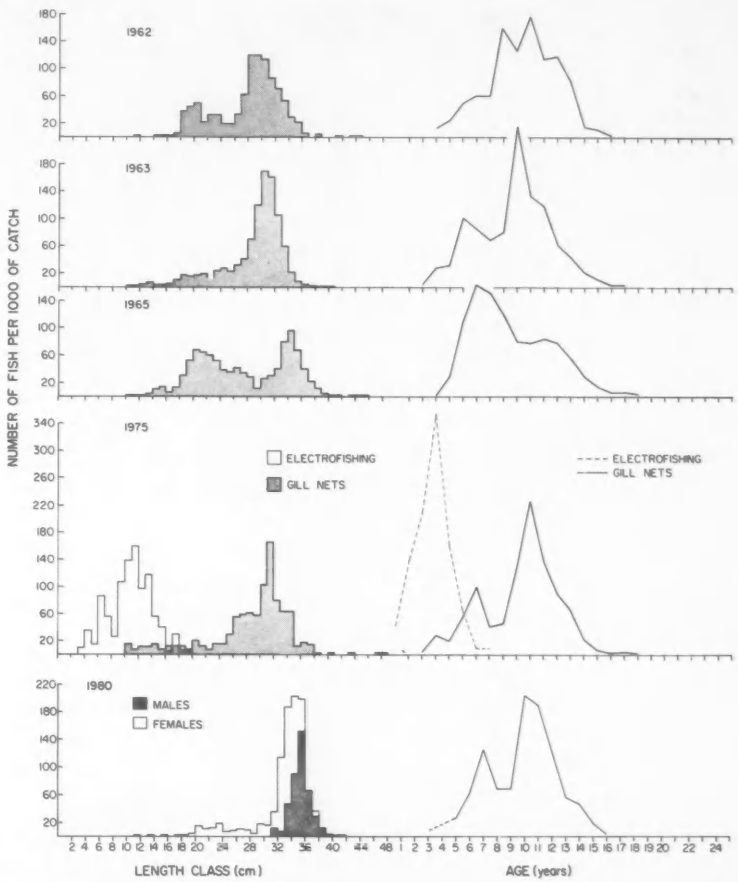

FIG. 12. Length and age distributions of Arctic charr, *Salvelinus alpinus*, in Keyhole Lake in 1962–80. The original modal configuration has reformed in 1975 after severe perturbation in 1962–65. By 1980 the mode has moved to the right and a great increase in uniformity has occurred. Age distributions generally tend to follow length distributions quite closely.

TABLE 4. Stock characteristics of Arctic charr, *Salvelinus alpinus*, from Keyhole Lake for the years 1962–80.

Year	Sample size	Mean weight (g)	Modal length (mm)	Mean weight at mode (g)	Mean age at mode (yr)	Age range at mode (yr)	Max. age (yr)	Catch per unit effort		Condition factor (K)
								No.	Weight (kg)	
1962	811	288	308	294	8.0	—	16	—	—	1.0037
1975	312	286	314	276	10.4	7–14	18	81	27.6	0.8312
1980	729	331	345	396	10.9	8–14	15	84	33.8	0.9662

5 yr. Although shown in the figure juxtaposed to the gillnet catches there is no implication that the actual numbers bear any relationship to each other; it is merely evidence for the existence of two distinct modes.

In 1980, conditions had changed appreciably; the modal length increased to 345 mm (identical to the larger modal value in 1965) and the whole configuration is much more tightly clustered; 76.7% of the total sample falls within the

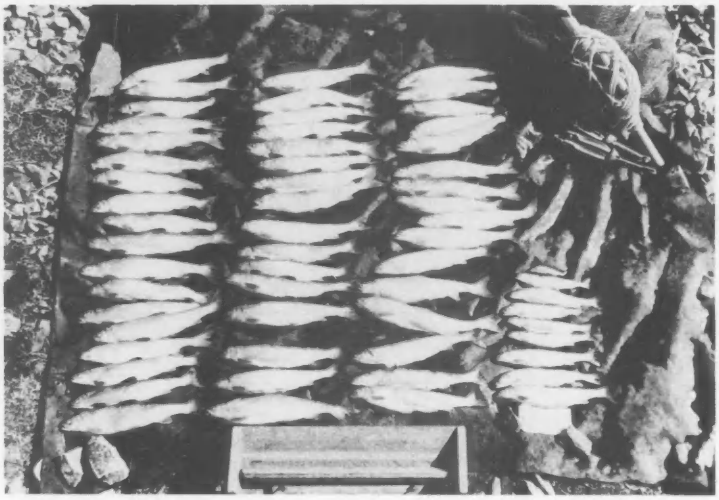

FIG. 13. Catch from one unit of effort (one 10-25 and one 10-60 net: 240 m of web) showing great uniformity of catch of Arctic charr, *Salvelinus alpinus*, from Keyhole Lake. (Photograph by J. S. Campbell.)

central 25-mm length class, and 85% falls within 25 mm on either side of the modal value. The exceptional uniformity of the stock is shown in Fig. 13. At the same time, the mean weight has increased from 286 g in 1975 to 331 g in 1980; the mean weight at modal length has also increased from 276 to 396 g. The apparent mean age at modal length has increased slightly from 10.4 to 10.9 yr (Table 4).

Between 1975 and 1980 there has been very little change in stock density with respect to charr over 250 mm in length. In 1975 the catch per unit effort of fish in this size range was 84; in 1980 it was 81. This is offset by a reduction, in 1980, of the number of fish in the smaller size range (<250 mm). As the density has remained constant the increase in mean weight represents a 16% increase in total biomass.

One of the most significant features of these results, extending over 18 yr, is the absence of oscillation in stock number. Even in 1965 following the heavy exploitation of the early years there is very little evidence of fluctuation. From 1965 to 1980, as far as can be observed, there has been a steady progression from a virtually "fished-out" lake in 1967 toward increased stock homogeneity that reaches an extremely high value in 1980.

LITTLE NAUYUK LAKE

In 1974 a sampling program on Little Nauyuk Lake was initiated using the experimental gear of Swedish manufacture (10-60 gill net). The result of this small sample (180 charr) yielded a strongly bimodal length distribution (Fig. 14) with modes at 215 and 345 mm; this bimodality, it was suspected, might reflect mesh selection. To obviate this possibility an additional net (10-25 gill net) was introduced reducing the interval between mesh sizes in the small and medium size ranges.

In 1975 an attempt was made to create a significant reduction in the stock in order to examine its reaction to heavy fishing pressure. A total of 2428 Arctic charr were removed using both the 10-25 and the 10-60 gill nets (Table 5). To test for selectivity, length frequencies of the catches were compared (Fig. 15) and found to be almost identical; modes occurred at 225 mm in both cases with means of 228 and 222 m, respectively. The major difference is that the 10-25 net outfishes the 10-60 net by a factor of 3 to 2. These results have been repeated in all subsequent years although with a reduction in the number of larger fish the 10-25 net has shown increasing superiority in relative catching capacity.

Mesh selection was further investigated in 1981 when the catch from individual mesh sizes was recorded (Fig. 16). The 10-60 net is now very much less effective but it still produces a mode at 225 mm; apart from the 10-mm mesh the remaining mesh sizes reveal little except that they are generally most effective over lengths between 200 and 290 mm. In the 10-25 net a mode in the 10-mm mesh is shown in the 100- to 130-mm length classes, an intermediate distribution in the 120- to 160-mm length range is given by the 12-mm mesh, and then the 16-, 19-, and 22-mm meshes all show modes at 225 mm. The 25-mm mesh shows a somewhat larger modal value at 250 mm.

The intensive gillnet fishery in 1975 gave rise to a highly symmetrical catch curve for length with a modal value of 225 mm (Fig. 14, 1975 Early). However, if the catches from 1974 and the July fishery in 1975 are combined, distinct bimodality appears with modes at 225 and 340 mm. It appears that a large number of the larger fish were removed in the early part of the fishery. This bimodality is magnified if numbers at length are converted to biomass (Fig. 17). The

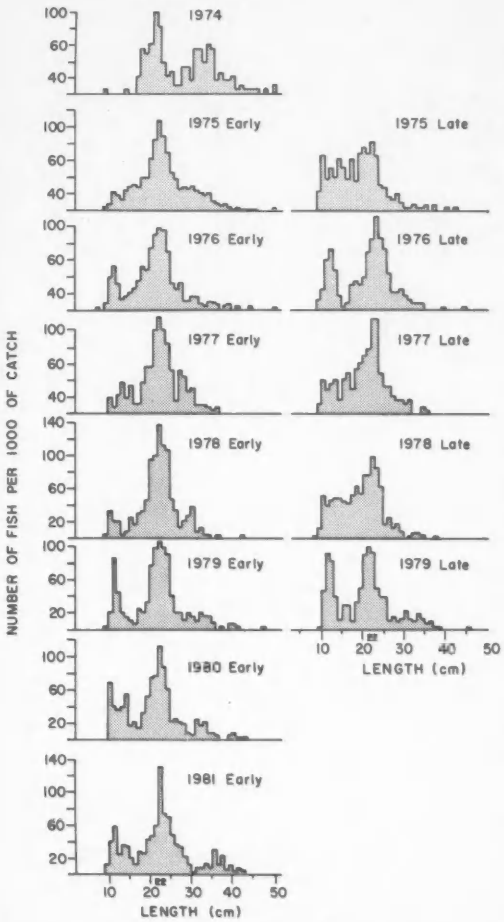

FIG. 14. Histograms of the length distribution of Arctic charr, *Salvelinus alpinus*, taken in the early (July) and late (August–September) fisheries in Little Nauyuk Lake. In general, there is a higher proportion of charr under modal size in the late fishery. The only deviation in modal size from a value of 225 mm is in the late fishery in 1976 when the modal value increased to 235 mm.

larger mode seems to be the result of an additional food source becoming available when the charr reach a length of 270 mm; only over this size is the large isopod, *Mesidotea entomon* (mean length 46 mm), found in stomach contents; above 270 mm it occurs in 78–80% of stomachs examined. The mode at 225 mm remains virtually constant over the succeeding years whereas the larger one at 340 mm disappears until 1981 when, following reduced exploitation in 1980, there are signs of a resurgence (Fig. 14).

A mode of small charr appears following the heavy fishery in 1975. At first its appearance is rather hesitant but by 1979 it appears to be permanently established in the 100- to 150-mm length groups. Modes of smaller fish at 40–50 mm are observable in the samples obtained by electrofishing (Fig. 18).

In the gillnet fishery interesting regularities occur each year. There is always a greater proportion of fish of less than modal length in the late fishery compared with the early one, as may be seen in the changes in mean weight, so that the stock enters the winter in a less uniform state than that in which it emerges the following spring. As these smaller fish must be present in the lake during the early fishery it is assumed that they are more readily caught because of increased movement in the fall. Increased movement in August may result from increased water temperature, increased food availability, and the protective covering of darkness that begins to develop at this time of the year.

Over the course of the investigations a very high degree of constancy is observable in the modal configuration. Only on three occasions did the modal length deviate from a value of 225 mm; each time, this deviation occurred in the late fishery. In 1976 and 1978 the value increased by 10 mm to 235 and in 1979 it fell to 215 mm. In each case a value of 225 mm was regained by the following spring. This regularity indicates the existence of a very effective mechanism for eliminating fluctuation and returning the stock to a set configuration.

The growth rate of individual fish, as in all the other lakes examined, shows extreme variability: in the modal length group (220–229 mm) charr between 6 and 17 yr of age were recorded in 1975 (Table 6). Individual variation remains great over the years, although mean age at modal length, after an initial drop from 11.2 to 9.4 yr, remains remarkably constant thereafter, fluctuating between 8.6 and 9.9 yr without any evident trend. Weight at length also shows considerable variation, charr of modal length (220–229 mm) in 1975 having a range of weight between 70 and 102 g. Condition increases appreciably and quite regularly over the open-water period. There is also a slight but rather ill-defined trend to improved condition over the years of observation that might be associated with reduced stock density. There is, however, little sign of reduction in the standard deviation of the mean condition factor such as might indicate more uniform nutritional conditions.

On the basis of the catch per unit effort, the density of charr was reduced by about one-half between 1974 and 1977 (Fig. 19; Table 5). On the basis of this reduction, and assuming the absence of recruitment over the 3-yr period, the initial stock was estimated to have been between 6500 and 7000 individuals over 179 mm in length. This is a density of 152–168 charr·ha^{-1}, a figure almost identical with that of the initial density in Keyhole Lake given by Hunter (1970) (163·ha^{-1}), although, it may be noted, the Keyhole Lake fish were considerably larger.

By 1982, a total of 7035 Arctic charr had been removed by gill nets from Little Nauyuk Lake, representing a harvest of 19.35 kg·ha^{-1} or an annual removal (over 9 yr) of 2.15 kg·ha^{-1}·yr^{-1}. In spite of these removals there is an indication that both individual size and catch per unit effort are beginning to increase. The configuration of the length frequency distribution in 1981 is almost identical with the

TABLE 5. Arctic charr, *Salvelinus alpinus*, catch data from Little Nauyuk Lake, 1974–82. Data in parentheses beside the modal value indicate the existence of a larger mode.

Year	Harvest			Catch per unit effort		Modal length (mm)	Mean weight at mode (g)	Mean weight (g)	Condition factor (K)
	No.	kg	kg·ha^{-1}	No.	kg				
1974	180	42.6	0.96	—	—	215 (345)	80	237	0.7038±0.0973
1975									
Early	2428	322.2	7.22	102	13.5	225	88	133	0.7757±0.0734
Late	288	23.1	0.52	144	11.4	225	94	80	0.8290±0.1014
1976									
Early	626	73.6	1.65	75	8.8	225	99	118	0.8724±0.0868
Late	229	25.0	0.56	78	8.5	235	108	109	0.9440±0.1140
1977									
Early	263	30.3	0.68	66	7.5	225	99	115	0.8701±0.0862
Late	243	22.7	0.51	112	10.5	225	103	93.4	0.9040±0.0930
1978									
Early	240	26.1	0.59	46	5.0	225	98	109	0.8622±0.0731
Late I	434	34.4	0.77	138	10.9	225	103	79	0.9000±0.0725
Late II	80	7.3	0.16	80	1.79	215	106	91	0.9270±0.0473
1979									
Early	243	27.9	0.63	26	3.0	225	95	115	0.8138±0.0995
Late	301	29.7	0.67	77	7.5	215	98	99	0.8388±0.1064
1980									
Early	362	37.8	0.85	30	3.5	225	89	105	0.7779±0.0768
1981									
Early	517	67.8	1.52	43	5.6	225 (360)	108	131	0.9437±0.0908
1982									
Early	601	92.9	2.1	51	7.7	235 (295)	120	154	0.9258±0.0699
Total	7035	863.4	19.35					122.7	

original one observed in 1975 although at a lower level of stock density. There is also a considerable increase in the overall mean weight of the catch (Table 5). These trends continue into 1982 accompanied by an increase in modal value from 225 to 235 mm and an appreciable increase in the mean weight at modal length. It very much appears that after a time lag of 6–7 yr compensatory changes in growth rate are beginning to show up.

In all the investigations age distribution tends to mimic the length frequency distribution, although the great variation in age-at-length ensures that relatively few individuals contribute to both the modal length and modal age classes. Without absolute precision in aging it is therefore extremely difficult to assess changing age composition from year to year and to gain insight into the processes operating. These differences from year to year become extremely blurred so that the virtual population, as indicated by the actual catch statistics, shows constant year class strength (Table 7) and almost constant mean age (Table 6). This result is unexpected in view of the high variability in the Arctic climate and its probable effect on year class strength.

Results from electrofishing, hoop net, and trap net operations provide age and length distributions below that given by the gill nets. Unfortunately there is no way in which these results can be related on a proportional basis.

A well-defined group of young-of-the-year was obtained by electrofishing the shoreline in August 1975 and 1976 (Fig. 18), the fish ranging in size from 38 to 51 mm in length by mid-August; 1-yr-olds at this time range from 71 to 92 mm and 2-yr-olds from 98 to 122 mm. Above 2 yr of age the length classes become very confused so that the 120- to 130-mm length class may contain young charr between the ages of 2 and 6 yr.

GAVIA LAKE

Gavia Lake is considerably smaller (17.4 ha) and shallower (z_m = 8 m, $\bar{z}$ = 2.9 m) than Little Nauyuk Lake. It has a reduction in water volume in winter of 45% and so approaches Keyhole Lake with respect to the possible occurrence of winterkill. However, no significant oxygen depletion has been observed at any time.

The program established for Gavia Lake demanded a single fishery immediately after breakup. A comparatively small

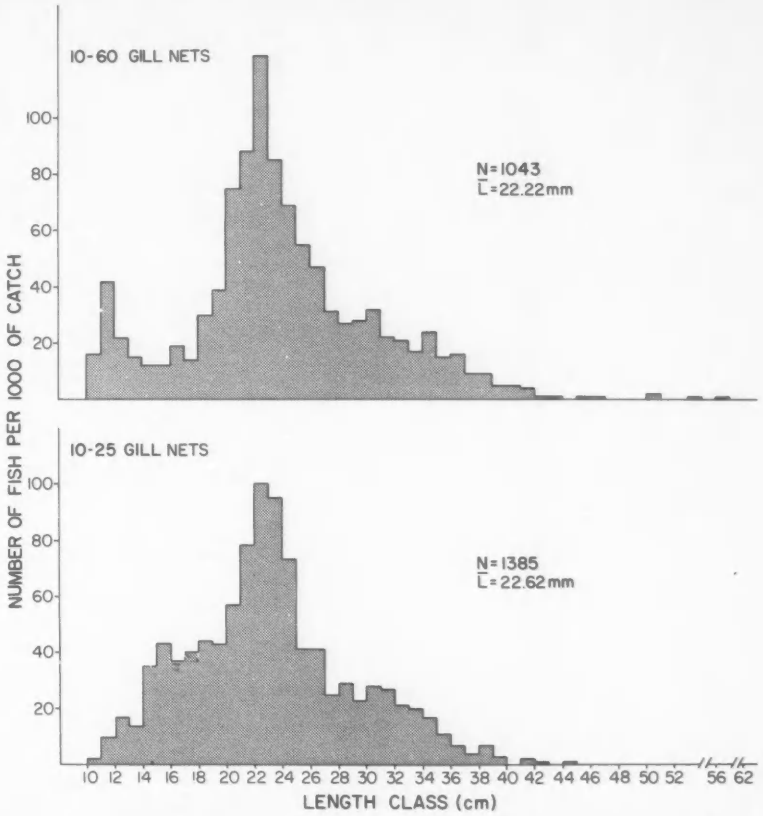

FIG. 15. Histograms of the length distribution of Arctic charr, *Salvelinus alpinus*, caught in 10-25 and 10-60 nets in Little Nauyuk Lake in 1975. Mesh sizes of the 10-25 net: 10, 12, 16, 19, 22, and 25 mm; mesh sizes of the 10-60 net: 10, 19, 32, 45, 57, and 60 mm.

sample of charr was removed from the lake in 1974 using a single 10-60 gill net. As in Little Nauyuk Lake, where the same net was used, a bimodal distribution was recorded although in Gavia Lake the modes were at 105 and 195 mm (Fig. 20; Table 8) compared with 225 and 345 mm in Little Nauyuk Lake. This distribution suggested that gill net selection was perhaps a factor in determining the distribution of the catch. To eliminate this probability the 10-25 gill net was introduced and fished simultaneously with the 10-60 in all further work.

In 1975 the stock showed a configuration completely different from that obtained in the previous year in that both length and age frequency distributions declined exponentially as length and age increased, the only case in which these theoretical expectations were met.

In 1976 a further radical change was indicated by a switch to a well-defined mode close to the original value of 195 mm. In 1977 the stock resumed a configuration almost identical with that exhibited in 1974, but devoid of the largest fish. This configuration was retained until the most recent observation in 1981, at which time the smaller mode appears to be decreasing with a return to the condition seen in 1976.

Almost no change is observable in the mean age determined for each length class, nor in the range of ages found in the modal length class (150–199 mm). Such regularity suggests that the number of rings on the otolith, or "annuli," are more closely correlated with length than with age. It is also of interest that the wide variation in age within each length class gives rise to such regularity in the mean values.

The largest fish in Gavia Lake, and the first to be removed, were cannibalistic in habit; this tendency toward cannibalism is not uncommon in charr stocks, particularly in lean environments (Skreslet 1973).

Electrofishing in 1975, 1976, 1978, and 1979 shows different patterns of distribution (Fig. 21) of small fish. In 1975 there is a mode exhibited at a length of 185–195 mm in a region of the gillnet catch that is poorly represented in the current year, but close to the modal values obtained in

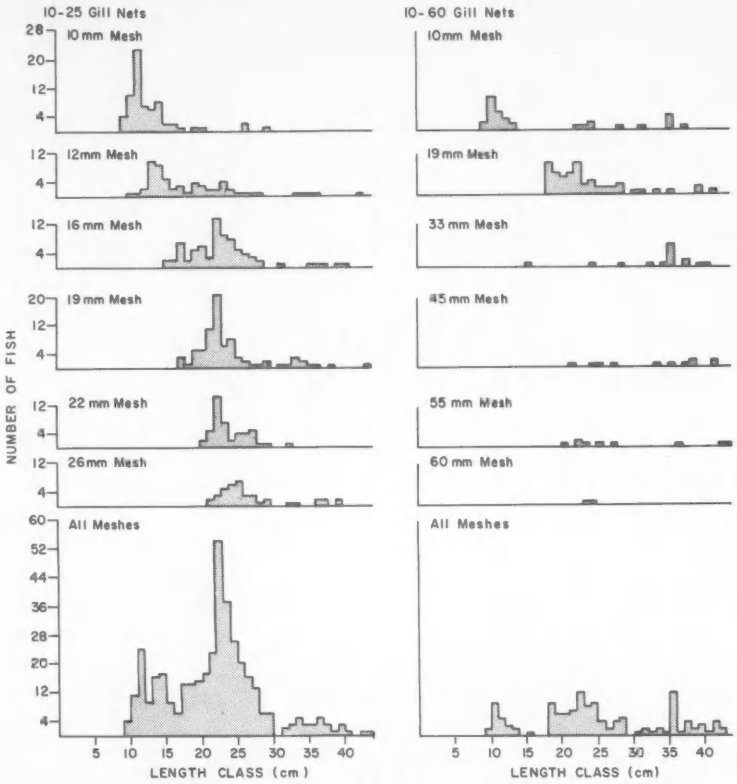

FIG. 16. Histograms of length distribution of Arctic charr, *Salvelinus alpinus*, taken in the individual mesh sizes in 10-25 and 10-60 gill nets in Little Nauyuk Lake in 1981.

the preceding and succeeding years. In 1976 this pattern is reversed with a well-defined mode, largely made up of 1-yr-old fish, at a length of 50–69 mm. In 1978 there is a mode at about 80 mm made up of 2-yr-olds. This apparently strong 1976 year class can no longer be recognized as a particularly abundant group in 1979; a new modal group of 1-yr-olds is, however, now recognizable at a length of 50–59 mm.

As in Little Nauyuk Lake certain features stand out very clearly. Most dramatic is the rapid change in configuration in the early years followed by the almost monolithic steadiness of the stock in subsequent sampling. The 1975 length frequency distribution is the only instance in which abundance declines with increasing size; maximum abundance is recorded at a midclass length of 105 mm, which is the lower limit of catchability of the gear. This distribution is apparently quite ephemeral, as, by the following year, all trace has disappeared. The unexpectedness of these changes was only exceeded by their rapidity. Also similar to the situation in Little Nauyuk is the constancy of the modal length value after 1976 and the rapid elimination of any minor fluctuation. There is a high degree of variation in age at modal length (Tables 8 and 9) in all years. However, after an initial reduction, the mean age settles down at a remarkably constant level for the remainder of the investigation; there is apparently no further increase in compensatory growth. In 1981 there was a reversal of the downward trend in catch per unit effort (Fig. 10) and a considerable improvement in condition factor.

NOTGORDIE LAKE

Notgordie Lake, the smallest lake examined, has a surface area of 7.1 ha and a maximum depth of 7 m. The winter reduction in volume amounts to 61.2% and in this it approaches Keyhole Lake.

An intensive sampling program was carried out in this lake between 12 and 26 July 1977; 926 charr were removed by gill net and 358 by hoop nets, poison, and electrofishing. By gill nets alone the equivalent of 130 fish·ha^{-1} were removed: this may be compared with the 144 fish·ha^{-1} removed from Little Nauyuk over the course of the 8-yr fishery and the 149 charr·ha^{-1} removed by gillnetting in

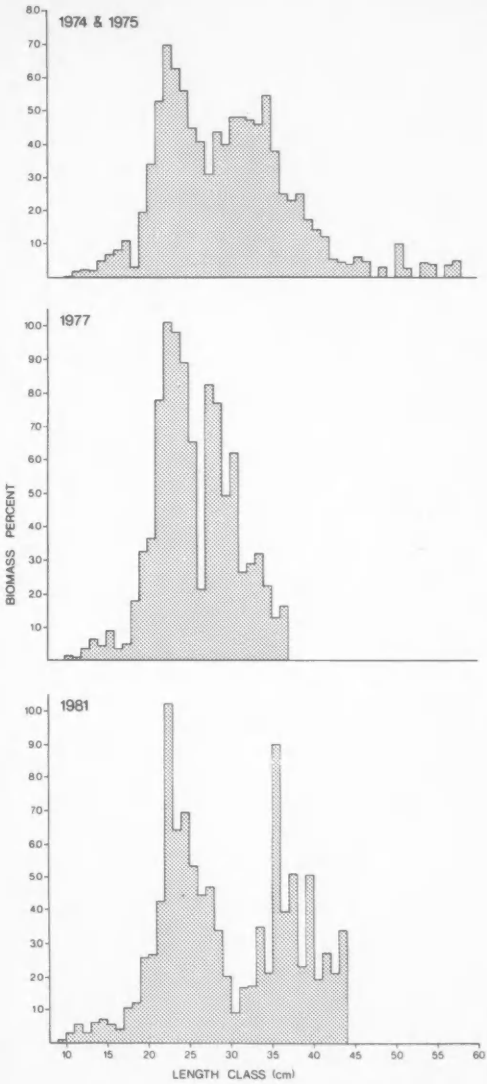

FIG. 17. Length distribution as related to biomass in the catch of Arctic charr, *Salvelinus alpinus*, from Little Nauyuk Lake. There is a marked bimodal distribution in 1974–75 that disappears in the middle years of the fishery and then is regained in recent years.

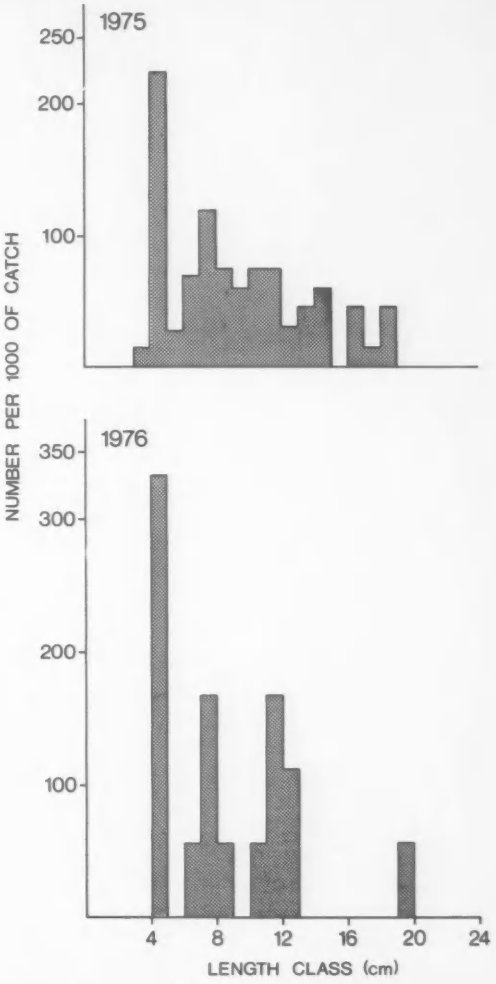

FIG. 18. Histogram of length distribution of juvenile Arctic charr, *Salvelinus alpinus*, taken by electrofishing in Little Nauyuk Lake.

Keyhole Lake between 1962 and 1967. However, there are great differences in the biomass: 7.1 kg·ha^{-1} (Notgordie), 24.3 kg·ha^{-1} (Little Nauyuk), and 43.8 kg·ha^{-1} (Keyhole). Catch per unit effort for gill nets in Notgordie Lake yielded 104 fish per net, a figure remarkably close to the initial value in Little Nauyuk Lake (102) and in Keyhole Lake in 1975 (103 fish per net) and 1980 (92 fish per net).

This very intensive sampling effort yielded essentially the same general configuration as obtained in the other small lakes (Fig. 22 and 23).

There is no suggestion that this lake has been sampled in totality. A large number of gulls were seen feeding after the sampling had been suspended, indicating a delayed action of the poison. Nevertheless, a considerable fraction of the total stock was examined. Test fishing after the operation yielded very few fish.

In Fig. 22 the total sample obtained is shown without any adjustment for gear type. There is a virtual absence of

TABLE 6. Little Nauyuk Lake, mean age of *Salvelinus alpinus*, stock at each 50-mm length class for the years 1975–81. The range of ages in the modal size group (200–249 mm) is given in parentheses.

	Length class (mm)									
	100–149	150–199	200–249 (range)	250–299	300–349	350–399	400–449	450	Overall mean	*N*
1975										
July	3.3	6.7	11.2(6–17)	10.7	14.4	16.0	17.8	23	10.3	377
1976										
July	2.8	6.2	9.4(5–17)	10.7	12.7	15.5	19.0	21.6	8.4	289
1977										
July	3.0	6.2	8.6(6–15)	8.4	10.8	14.0	—	—	7.8	146
August	2.8	5.1	9.1(6–17)	9.0	10.7	13.0	15.0	—	7.2	320
1978										
July	2.1	5.4	9.1(6–14)	9.6	9.1	15.0	16.0	—	8.0	154
August	3.1	5.1	9.4(5–14)	9.9	10.1	16.0	—	—	7.4	121
1979										
July	3.4	6.3	9.6(5–16)	9.7	10.2	13.2	16.3	11	8.5	183
August	3.4	5.8	8.9(5–14)	10.0	9.8	11.2	—	16	7.0	98
1980										
July	3.4	6.4	9.9(6–17)	9.9	11.6	12.3	15.6	—	8.4	120
1981										
July	3.1	6.5	9.1(4–15)	8.7	10.6	12.1	15.3	—	8.4	317

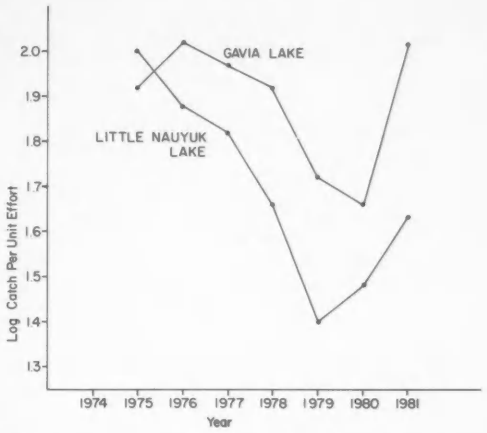

FIG. 19. Changes in the catch per unit effort of Arctic charr, *Salvelinus alpinus*, in Little Nauyuk and Gavia lakes 1975–81. Values of the catch per unit effort have been transformed to logarithms.

large fish; only two were captured: one 445 mm and the other 325 mm. The major mode is at 200 mm (mean age = 8.0 yr) and there are smaller modes at 110–120 mm (mostly 3- to 6-yr-olds) and 30–40 mm, the latter composed of young-of-the-year (0+ yr).

CHAR LAKE

Studies carried out by MacCallum and Regier (1981) during the course of the IBP program in 1970 and 1971 gave an estimated total of between 18 000 and 19 000 fish in the lake; as the lake is 52.6 ha the standing crop is about 360 individuals $\cdot$ ha^{-1}, or 9.23 kg $\cdot$ ha^{-1}. The charr are numerous but of small size and great age. Using angling as their major sampling technique in 1970 MacCallum and Regier obtained a unimodal length frequency with a modal value of 150 mm; in 1971, using trap nets, a similar distribution was obtained but with a slightly smaller modal value at 145 mm. Gillnetting, they believed, tended to select for larger fish. They estimated the mean age of a charr 150 mm in length to be 13.7 yr.

In 1982 the opportunity presented itself to test the standard 10-60 and 10-25 gill nets against these results. Again a unimodal length frequency distribution was obtained, but having a slightly smaller modal value (135 mm) than that previously observed (Fig. 24). Although a considerable period of time had elapsed since the previous observations there seems little possibility that major changes have occurred. Ages are still very great for the length and are very similar to those obtained previously; the mean ages of charr in 1982 of 135, 145, 155, and 165 mm were found to be 9.9, 11.8, 11.6, and 15.2 yr, respectively.

VALIDATION

The question inevitably arises as to whether these results are truly representative of the stock in each lake or whether they are merely an artifact of the sampling procedure. Specifically, such results (Johnson 1972, 1976) have frequently been attributed to gill net selection. Gill nets are, in fact, extremely efficient and far more effective than other gear in the circumstances; hence, it is extremely difficult to validate results by alternative methods. To dismiss such results as being due to gillnet selection is to place more confidence in the completely hypothetical population remaining in the lake than in the actual observations in hand. Unless gillnet selection, at the appropriate level, can be demonstrated, its invocation leads to an infinite regress against which no argument can prevail; it also leads to the dismissal of some extremely interesting features of the structure of unexploited populations. No matter how precise the observations, we shall never obtain, in biological measurement, the degree of correspondence with prediction that we might wish; it is therefore the regularity of occurrence of patterns that must be sought rather than precise correlations.

When the 10-25 and 10-60 gill nets are fished together as a unit of effort (240 m of web) over a wide geographical area, a wide range of modal values has been obtained, each value apparently characteristic of the particular lake concerned. Not only Arctic charr but all northern species as stressed by Magnin (1977) exhibit similar characteristics. The modal length values for charr range from 100 mm in Gavia Lake (in 1975), 135 mm in Char Lake through 225 mm for Little Nauyuk Lake, to 320 and 340 mm for Keyhole, Nelson, and Hazen lakes. Lengths over which maximum abundance occurs in some lakes are represented by troughs in the catch curves from others. Within individual lakes, modal size remains remarkably constant; very small differences between neighboring lakes have been maintained over many years with no overlapping (Fig. 14 and 20).

A comparison of the total catches from the 10-25 and 10-60 gill nets in Little Nauyuk Lake in 1975 (Fig. 15) shows remarkably little difference in the catch curves obtained, in spite of the great difference in their mesh composition. The major difference is in the greater catching efficiency of the 10-25 net, a difference that increases considerably as stock density is reduced (Fig. 16).

When the length frequency distribution of the catch from the individual mesh sizes is examined it is apparent that a degree of mesh selection does occur, as exemplified in the results from Nelson and Little Nauyuk lakes (Fig. 10 and 16). The smallest mesh size captures the smallest fish down to a limit of 100 mm, the lower limit of catchability; that the gear is very effective at this lower limit is shown by the catch from Gavia Lake in 1975 where 100–110 mm was the most abundant length class present. Intermediate mesh sizes appear to be very effective over certain length groups but show no great capacity to select for a specific size, as the modal size remains almost constant. The largest mesh sizes capture fish in the same size range as those in the intermediate mesh sizes, but at a very much lower efficiency.

In Char Lake, fishing with the 10-25 and 10-60 gill nets yielded a smaller modal value than was obtained either by trapnetting or angling. Unfortunately, it is not possible to decide whether the results are due to gear selection or whether there has been a slight change in stock size. Development of

TABLE 7. Year class strength of Arctic charr, *Salvelinus alpinus*, in Little Nauyuk Lake, 1975–81, with cumulative totals of individuals of each age taken in the fishery.

	Age (yr)																								
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1975		68	78	102	121	134	114	175	238	206	189	291	226	126	102	83	73	46	29	12	5	5	2	2	2
1976	1	69	85	13	40	79	80	87	71	72	56	65	49	26	10	10	11	4	6	3	3	—	—	—	2
1977	4	19	55	32	19	49	55	69	66	37	39	17	18	13	6	1	1								
1978	30	29	73	71	51	40	68	97	97	75	60	27	17	11	4	5	2								
1979	—	—	72	24	36	30	39	50	50	84	54	45	15	33	—	6	—	—	3	3					
1980	—	—	49	33	9	37	18	27	46	30	43	27	9	3	9	9	12								
1981	—	11	23	19	10	18	55	27	28	39	30	26	11	13	3	1	—	1	1	—	—	1			
Year class strength							323	311	243	394	462	533	434	410	397	339	292	376	264	139					
Year class							1974	1973	1972	1971	1970	1969	1968	1967	1966	1965	1964	1963	1962	1961					

the airport runway within the Char Lake drainage basin may have occasioned some small changes in the lake environment, but all other activities in the watershed have been prohibited, as Char Lake now provides the water supply for the Resolute Bay townsite.

It is also apparent that larger fish tend to be captured in the earlier stages of the fishery. This is recognizable in all the lakes fished over a prolonged period. The major effect in the early stages is merely to reduce the variances on the length distribution of the catch, a feature also observed by Dempson (1982) in the Labrador charr fishery.

Differential recruitment from the peripheral areas of the niche to the central region occupied by the "effective population," or "establishment," presumably does occur. The shape of the catch curve for age indicates underrepresentation of fish in the younger age classes, if, as is customary, the instantaneous curve is taken to represent the passage of a single year class through the population. That this is justified is indicated by the virtual population for Little Nauyuk Lake (Table 6) where recruitment at an almost constant level from each year class is observed. As fish cannot begin their lives at an age of 5 or 6 yr, it is presumed that a considerable number of small but relatively old fish remain in the peripheral regions until opportunity occurs for them to join the establishment. Fish of a length between 100 and 150 mm in Little Nauyuk Lake may be between 2 and 13 yr of age (Johnson 1980); the difficulty arises through the impossibility of sampling the peripheral regions in a proportional manner. As is shown in the difference between the early and late catches in Little Nauyuk Lake there is a considerable increase in the movement of small fish later in the season; this change in representation does not, however, alter the modal value.

A further difficulty is presented by the aging of northern fish; as Power (1978) suggested, the age of northern fish may generally be underestimated. There are anomalies in the data that suggest that this may well be so. This is not to suggest that the number of growth rings, or "annuli," of the otolith have been counted wrongly — in general there is good agreement between readers — but merely that the vicissitudes of life in a lean environment may preclude the annual deposition of material in a manner that makes all the individual rings identifiable using current techniques.

In spite of the high degree of variability in age-at-length, mean values and age distributions of the population show considerable regularity from year to year; in fact, this regularity is greater than might be expected if the population remains at constant length. In general, age distributions tend to mimic length distributions; this can be seen clearly in the age and length changes in Gavia Lake (Fig. 20) between 1975 and 1977. There is the suspicion that the number of growth bands on the otolith is more closely correlated with length than it is with chronological age. The regularity of the contribution of the various age classes to the Little Nauyuk Lake establishment is, in itself, a matter of suspicion in view of the variation in the climate of this region. Particularly early years have been shown to correspond with large year classes in Willow Lake, the nursery lake for the anadromous charr stock of Nauyuk Lake (a neighboring system, completely independent from Little Nauyuk Lake). On the other hand, there is evidence that the number of otolith bands

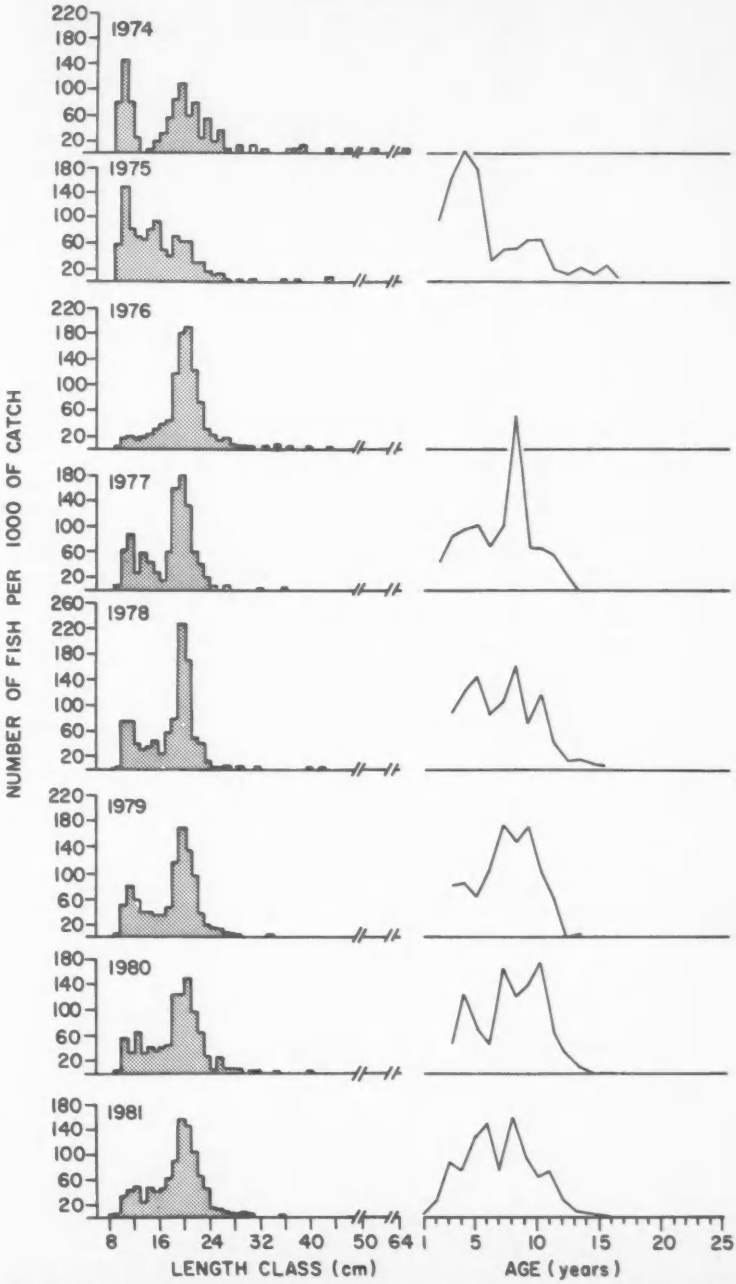

FIG. 20. Histograms of length and age distributions of the catch of Arctic charr, *Salvelinus alpinus*, from Gavia Lake from 1974 to 1981. The 1974 data suggest the effect of mesh selection, which is apparently eliminated in 1975 with the introduction of additional gear. From a curve that approximated a negative exponential distribution in 1975 a modal configuration is assumed in 1976 that is retained for the duration of the observations. Age distribution closely follows length distribution.

TABLE 8. Gavia Lake catch data for Arctic charr, *Salvelinus alpinus*, 1974–81 (*data for 10-25 nets only).

	Harvest			Catch per unit effort						
				No.						
	No.	kg	kg·ha^{-1}	<159	>159	Weight (kg)	Mean weight (g)	Mean length (mm)	Modal length value (mm)	Condition factor (K)
1974	170	16.9	1.0	—	—	—	103	183	195	0.8481
1975	391	19.3	1.1	83	48	10.3	39	152±78	105	0.9473
1976	446	34.9	2.0	166	130	13.0	79	200±43	205	0.8848
1977	462	23.3	1.3	94	62	4.7	50	171±44	195	0.8457
1978										
July	397	24.1	1.4	84	55	5.1	61	179±52	195	0.8252
August	311	17.6	1.0	155*	—	8.7*	57	161±54	195	0.8801
1979	425	24.1	1.4	53	37	3.0	57	179±44	195	0.8711
1980	365	24.3	1.4	46	34	3.1	69	187±51	205	0.8447
1981	511	34.7	2.0	127	97	8.7	68	187±41	195	0.9500
Total	3478	219.2	12.6				63.0			

does approximate the true age; for example, the charr of Keyhole, Nelson, and Hazen lakes each exhibit a modal value between 320 and 340 mm; the estimated mean age of the modal length group increases regularly with latitude, as might be expected. A similar increase in age, at a given length, with increasing latitude was observed by Dempson (1982) for the Labrador charr.

These difficulties are to some extent resolved if the growth rate in charr is regarded as length dependent rather than age dependent, a feature recognized in the rainbow trout, *Salmo gairdneri*, of British Columbia by Larkin et al. (1956). If this is the case then peak distributions represent lengths over which growth is relatively slow whereas the troughs are lengths over which growth is fast. In the anadromous population of Arctic charr at Nauyuk Lake such a process has been verified; the sea-going fraction of the population is strictly bimodal with modes at 220 and 600 mm, as determined by observation of the passage of the total sea-going stock through a counting fence. Marking of individual charr in the smaller mode indicates that growth rate increases up to a length of 300 mm and then declines as the upper modal value is approached (Johnson and Campbell 1976; Johnson 1980).

This process, reflecting a decline in growth rate as the modal size is approached, can most aptly be described as "piling-up"; but, in view of the great variation in age at modal length, it can scarcely be considered the resultant of a regular decline in growth rate with increasing age, in conjunction with natural mortality. It appears to be a process arising out of interaction between individuals and therefore under internal group control.

In view of these observations the hypothesis appears to be fully substantiated: homeostatis is maintained in face of the environmental variation normally experienced, as well as in face of considerable external perturbation imposed by a fishery; when perturbation is eliminated the stock returns to its original configuration, without oscillation.

Discussion

Verification of the hypothesis establishes the stock as a functional, coherent, self-regulating unit. These are the characteristics of a dissipative structure (Prigogine 1978, 1980; Glansdorff and Prigogine 1971; Prigogine et al. 1972; Nicolis and Prigogine 1977; Johnson 1981; Wiley and Brooks 1982). Dissipative structures can exist only in nonequilibrium conditions in which energy and entropy are exchanged with the external environment; they exist as structures in the energy flow pattern and survive only on energy input dissipated in the maintenance of that flow pattern (Neumann 1978). Their most significant characteristic is that they tend to assume a state of least dissipation of energy when allowed to remain unperturbed. When perturbed the rate of dissipation increases but the system eventually settles down to a new state of least dissipation commensurate with the new conditions (Prigogine 1978); if the perturbation is removed then the system returns to its original state of least dissipation. Least dissipation represents maximum accumulation of energy (biomass) relative to the energy input. This is equivalent to imposition of maximum time delay on energy flow through the structure for a given state of complexity.

The characteristics of a dissipative structure are sufficient to explain the observations on the autonomous charr stocks in Arctic lakes. A state of least dissipation, with respect to the stock as a whole, is readily recognized by the high degree of length uniformity of the component individuals, irrespective of their age, large biomass relative to energy input, great mean age, and an indeterminate age at death. If such a configuration is to be maintained over time the number of juveniles required for replacement purposes will be small, being only slightly greater than the number of recruits needed to compensate for adult mortality. This configuration is, in fact, simply an expression of the recognized process in which the dominant species tends toward a state in which its production/biomass (P/B) ratio assumes a minimum value (Margalef 1963, 1968). The P/B ratio, as pointed out by MacArthur (Leigh 1965), is dimensionally equivalent to the reciprocal of the mean life span; hence, a tendency toward a decreasing value implies a tendency toward a longer turnover time or a decrease in the rate of dissipation relative to the biomass accumulated. It must be stressed that in the present formulation it is the individual species that proceed toward a

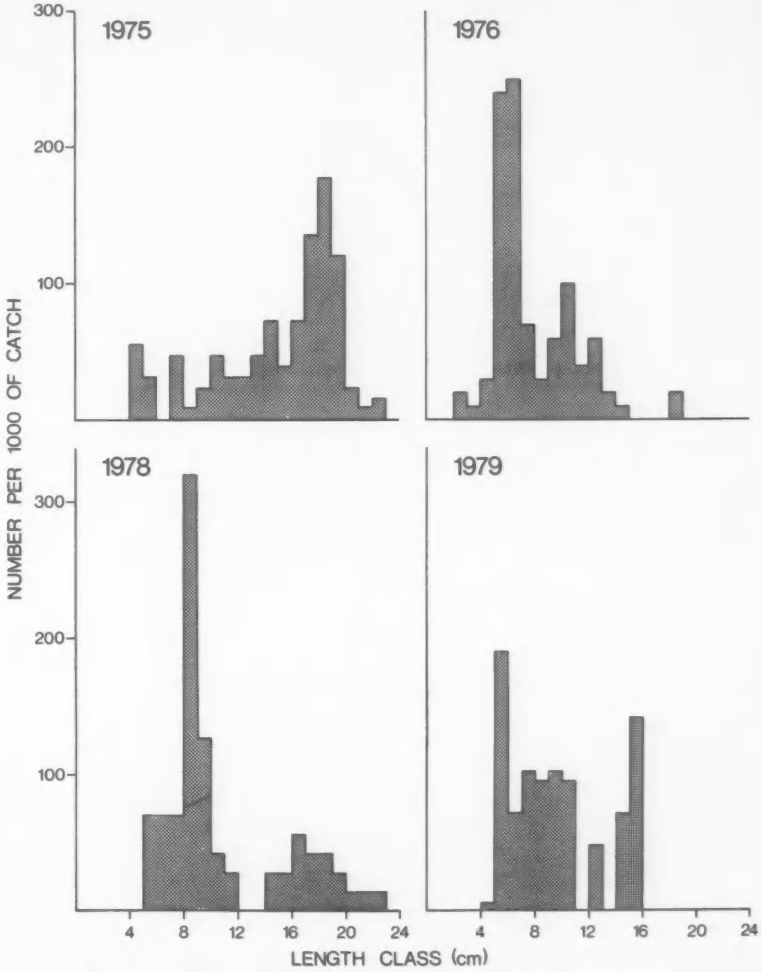

FIG. 21. Histograms of the length distribution of Arctic charr, *Salvelinus alpinus*, taken by electrofishing rocky shorelines in Gavia Lake in 1975, 1976, 1978, and 1979. The inverted form of the plot, compared with the gillnet catches (Fig. 20) in 1975, is interesting but difficult to explain.

TABLE 9. Gavia Lake, mean age of *Salvelinus alpinus* stock at each 50-mm length class, 1975–81. The range of ages in the modal length class (150–199 mm) is given in parentheses.

	Length class (mm)										
	0–99	100–149	150–199 (range)	200–249	250–299	300–349	350–399	400–449	450	Overall mean	*N*
1975	3.0	3.4	6.5 (4–13)	9.9	11.5	12.8	14.1	14.0	16	6.1	62
1976	—	—	7.8 (6–11)	—	—	—	—	—	—	7.8	13
1977	—	3.7	7.6 (4–12)	8.4	8.0	14.0	12.0	—	—	6.8	70
1978	—	3.8	7.1 (4–11)	9.3	10.7	10.0	15.0	14	14.5	7.0	189
1979	—	4.4	6.8 (5–11)	8.7	10.1	11.0	—	—	—	7.5	172
1980	3.0	4.3	7.9 (5–13)	9.2	10.1	14.0	12.0	—	18	7.8	362
1981	1.6	3.5	6.8 (4–15)	9.1	9.9	7.5	16.0	—	—	7.0	511

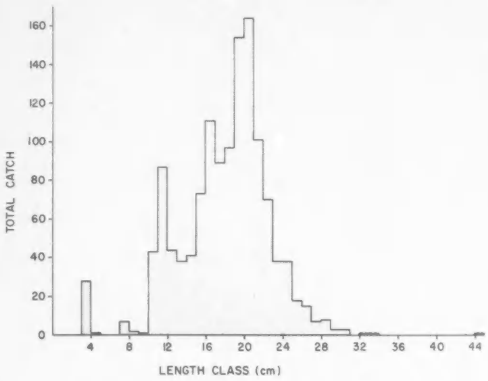

FIG. 22. Histogram of the length distribution of Arctic charr, *Salvelinus alpinus*, taken in Notgordie Lake by gill nets, hoop nets, and poison in 1977.

least value of their P/B ratios, not, as Odum (1969) suggested, the system as a whole. It is the effect of the dominant species (in which the trend can be most clearly recognized) that masks the underlying effect of interspecific interactions that, in actuality, tend to stimulate increased energy flow rates (Johnson 1981).

While it has been recognized for some time that an individual organism has many of the characteristics of a dissipative structure (Prigogine and Waime 1946), it is perhaps somewhat more difficult to understand the mechanism whereby individuals, together, function as a dissipative unit. This can be readily explained in terms of statistical mechanics, as developed by Soodak and Iberall (1978), under the doctrine of homeokinesis. Homeostasis is achieved in a bounded system "by means of a dynamic regulation scheme whereby the mean states of internal variables are attained by the physical action of thermodynamic engines." Homeokinesis ensures that a group of like-individuals, interacting within the boundaries of its niche, equipartition the energy available. Equipartitioning of the energy ensures that if the individual has the character-

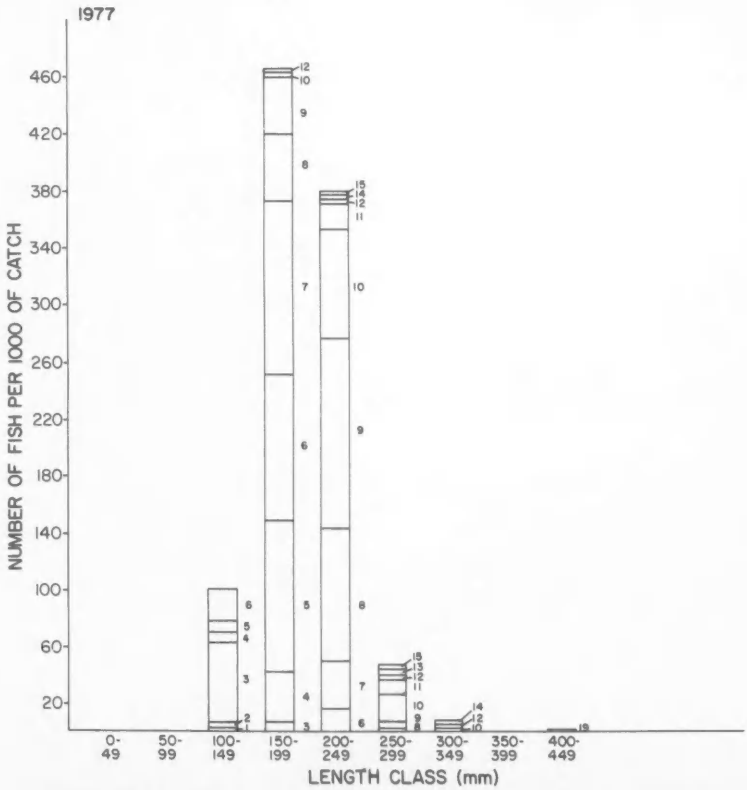

FIG. 23. Histogram of combined length and age distribution of Arctic charr, *Salvelinus alpinus*, taken in gillnet catches in Notgordie Lake in 1977.

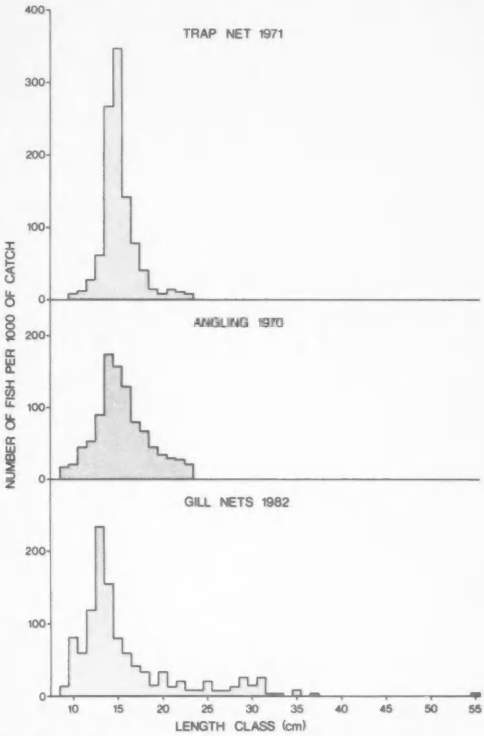

FIG. 24. Histogram of length distribution of Arctic charr, *Salvelinus alpinus*, from Char Lake. There is an apparent decline in modal length depending on the method employed although the results were not obtained simultaneously.

istics of a dissipative structure then the group of individuals, functioning as thermodynamic engines, will, together, form a single dissipative unit and proceed to a state of least entropy production.

A homeostatic mechanism maintaining an accumulation of energy at a constant level implies the existence of organization. Organization, as discussed by Pittendrigh (Mayr 1976, p. 391), implies not only an increase in order but a goal or end point towards which the system proceeds. Order in fish stocks is evident in their uniformity; the ultimate goal of an ecodeme, or interacting group of like-individuals, is the best integration of energy acquisition, energy equipartitioning, and conservation that it can attain. In that changes in the capacity to acquire energy occur only over evolutionary time, the proximate goal of the ecodeme is the attainment of a state of least dissipation or least value of its P/B ratio. Organization thus reflects a goal that is attained through reduction in the rate of energy flow; this is, in effect, the equivalent of a damping mechanism. The existence of a damping component within a stock thus implies that the stock functions as an organized whole and not a group of independently acting individuals.

Stock homeostatis and biomass accumulation are fundamental characteristics of the fish stocks of the lakes examined; of particular interest are the results from Keyhole Lake. Ten years after severe depletion, the charr population had returned to its original configuration, apparently without significant oscillation; in the following 5 yr it showed a strong positive change towards increased uniformity and reduced dissipation. The considerable increase in biomass reflects reduced dissipation, since it is unlikely that a new or augmented food source could become available over the time being considered. The increase in uniformity is believed to have resulted from the sampling in 1975 having preferentially removed most of the larger fish, allowing the development of greater uniformity than can be sustained naturally. Habitat variation and individuality apparently allow the emergence of relatively few fish much larger than the modal size and usually supported by cannibalistic habits (Fig. 22, 23, and 24); the effect of removing these large fish creates much greater cohesion within the remaining stock. This can be clearly seen in Gavia Lake in 1975 and 1976 (Fig. 20); in 1975 the stock in this lake showed a maximum abundance at a length of 100 mm, the lower limit of catchability; removal of the larger fish, of which there seemed to be a greater number than usual, allowed a new modal configuration to develop at a value of 195 mm, this being retained with only very minor change until 1981, when sampling was temporarily suspended.

Similar homeostatic mechanisms have been found to exist in all plant and animal species investigated and therefore, by extension, appear to be universal. Gilpin et al. (1976) demonstrated the existence of a damping mechanism in laboratory populations of mosquitoes; Hassell et al. (1976) found that in species with little overlapping of generations, there is a monotonic return to a stable equilibrium following disturbance; they concluded that most natural populations exhibit similar behavior. Thomas et al. (1980) showed that although the models frequently used in population dynamics studies allow the possibility of chaotic growth (given the allocation of suitable values to parameters) they could not induce such chaos in laboratory populations of *Drosophila*. They suggested that group selection is necessary for the evolution of such a communal damping mechanism. Mueller and Ayala (1981) found similar homeostatic mechanisms in *Drosophila melanogaster* stocks but denied the necessity of group selection as a causative mechanism. Roughgarden (1979) could find no evidence of chaotic growth in the vertebrate stocks he examined.

One of the most detailed studies demonstrating the existence of a damping mechanism in natural populations is that of Southern (1970a, 1970b) on the tawny owl, *Strix aluco*, in Wytham Woods, Oxford. Following an exceptionally severe winter in 1947, the number of tawny owl breeding pairs on this 525-ha estate was reduced to 16. Gradual recovery of the stock took place between 1947 and 1955 as the number of pairs climbed to an asymptotic level of 30, where it remained until the work was terminated in 1959. In spite of considerable fluctuation in food availability and the number of potential recruits, the recovery process was monotonic. Although final density is controlled through the operation of a territorial system, territories are not, apparently, rigid in their boundaries: individual territories tend to decrease in size as the number of pairs increases toward the asymptotic value. It

is of great interest that population control is effected at the time when juveniles attempt to secure a territory; potential recruits failing to find a territory were forced to migrate out of the system and were frequently found later to have died of starvation. This mechanism is the most sensitive with respect to control of population density and is essentially the same as that which I hypothesized as occurring in the regulation of northern fish stocks (Johnson 1976), the main difference being the absence of any specific territories in the fish populations.

The operation of a strong damping mechanism can also be discerned in the lake whitefish, *Coregonus clupeaformis*, stocks of Lake Winnipeg (Davidoff et al. 1973). During a period of stock depletion, the catch per unit effort declined gradually displaying none of the irregularities that might be expected to result from differences in year class strength. Comparable smooth declines are recorded for Little Nauyuk and Gavia lakes (Fig. 19) and for the decline in fish catches in the Great Lakes (Smith 1968). Conversely, the failure of such regulatory mechanisms seems to be evident in the wild oscillation in population density of the blue pike, *Stizostedion vitreum glaucum*, in Lake Erie, immediately prior to its demise (Regier et al. 1969).

Harper (1967, 1969, 1977) discussed the question of self-regulation of density in plant populations and recognizes its existence in both experimental and natural conditions. In the field, Tamm (1948, 1956) concluded that apparently stable vegetation is dynamic in character. In the course of long-term studies on vegetation in Scandinavia he showed that the abundance of many species may remain quite constant in spite of high turnover rates among individuals. He also found that the disappearance of a species is a gradual process taking place over many years and not a sudden response to extreme conditions.

It is concluded that the phenomenon of organization within a stock is universal and is generally recognized in such terms as "carrying capacity" (Errington 1946, 1956) and "equilibrium density" (MacArthur and Wilson 1963, 1967; Caswell 1982) as well as the whole question of "self-regulation" in animal populations (Nicholson 1933, 1954; Nicholson and Bailey 1935; Lack 1954; Krebs 1978), the features of "*r*- and *K*-selection" (MacArthur and Wilson 1963, 1967), and the botanical "climax." An attempt to generalize the phenomenon resulted in the "logistic" curve (Hutchinson 1978), which is predicated on the existence of a goal, the asymptotic value for the population, and the existence of an internal regulatory mechanism. The logistic curve, frequently used in population models, is, however, at best only an approximation to the true state of affairs, since it is a product of mathematical order and does not reflect the interactive processes inherent in organization.

The characteristics of the charr populations in small Arctic lakes, and their behavior under perturbation, provide considerable insight into the method of operation of the homeostatic mechanism as exhibited in *r*- and *K*-selection and the climax.

THE *r*- AND *K*-CONFIGURATIONS

The capacity of a species to respond to exploitation, as discussed by Adams (1980), is a function of its life history characteristics as reflected in the extent to which it has been subject to *r*- or *K*-selection (MacArthur and Wilson 1963, 1967; Pianka 1970; Gadgil and Solbrig 1972). It is hypothesized that in stable environments, species are selected for stability, low reproductive capacity, and low replacement rates leading to a steady state or "equilibrium" (*K*). In a fluctuating environment, selection is considered to be towards higher rates of turnover and increased intrinsic rates of reproduction (*r*). This concept has recently come under criticism; R. F. Green (1980) maintains that *r* and *K* are not strictly comparable, as *r* is a function of life history parameters whereas *K* is not. Schaffer (1979) believes that *r* is not justifiably equated with reproduction nor *K* with postbreeding survival.

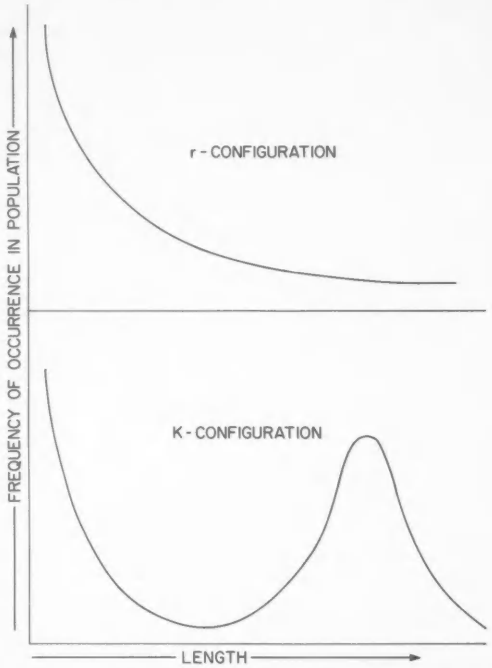

FIG. 25. Postulated form of the *r*- and *K*-configuration. The extreme form of the *r*-configuration is represented by a negative exponential curve indicating maximum energy flow rate through the population, a form probably seldom, if ever, achieved in natural populations. The *K*-configuration represents the size distribution of a dominant species in which recruitment is reduced to a low level commensurate with replacement needs. This form of curve is typical of the dominant species Arctic charr, *Salvelinus alpinus*, or the tree dominants of temperate forests. Energy flow through the population is reduced to the lowest level attainable.

These anomalies can be resolved if *r* and *K* are regarded as descriptive terms rather than as specific identities. Every species, it may be assumed, has both an *r*- and a *K*-component. The *K*-component represents the basic tendency of a species to assume a state of least dissipation and to exert maximum damping effect commensurate with its status in the eco-

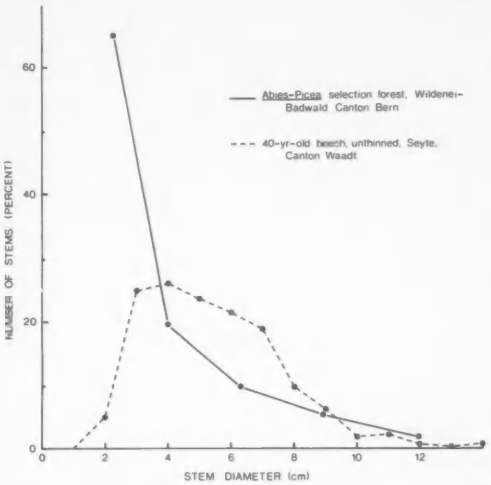

FIG. 26. Diameter distribution of stems in *Abies–Picea* forest in Wildenei-Badwald, Canton Bern, created by careful selection and thinning, to induce maximum sustained yield, compared with natural, unthinned beech, *Fagus sylvatica*, forest at Seyte, Canton Waadt, Switzerland. (Redrawn from Jones 1945.)

system hierarchy. The dominant species is the one that achieves the best integration of energy acquisition and conservation and exerts the maximum damping moment on the whole system. The dominant species is the one that approaches most closely to a steady state and manifests a *K*-configuration. A *K*-configuration is adopted when the rate of energy flow reaches a minimum value relative to the biomass, a state of least dissipation, as exemplified by the charr stocks. An *r*-configuration is one that represents maximum energy flow rate, where growth is age dependent so that size distribution follows the same type of negative exponential curve as mortality (Fig. 25). Rapid turnover times allow the organisms, as a group, to track closely the energy availability. Organisms may be regarded as being "forced" into an *r*-configuration in response to grazing or predation pressures and a fluctuating energy input. It is unlikely that the ultimate *r*-configuration, represented by the negative exponential curve for size distribution, is ever realized except by carefully controlled manipulation in agriculture or forestry.

When forests are managed for maximum sustained yield it is held that maximum rate of return is obtained where the diameter distribution is maintained in the "inversed-*J*" configuration (Meyer 1952). This type of distribution is widely recognized in Europe under the apellation "forêt jardinée," "blenderwald," or "plenterwald" (Jones 1945); it can only be maintained by careful felling and thinning. An example of the inversed-*J* distribution is shown in Fig. 26, as obtained from a stand of fir, *Abies* sp., and spruce, *Picea* sp., in Switzerland; it is contrasted with an unthinned stand of 40-yr-old beech. The structure of these two forests provide nearly perfect examples of the *r*- and *K*-configurations, the one leading to most rapid energy flow and the other to energy accumulation. Jones (1945) stated that the merits of the blenderwald system are a matter of active debate amongst foresters.

The *K*-component represents accumulation and damping; the *r*-component represents response time, the capacity to accommodate to fluctuations both of a short-term and long-term nature. These characteristics determine the stability of the ecodeme. A species with a strong *K*-configuration will absorb short-term fluctuations and show little change, but without some *r*-component it would not be able to adapt to secular change or external perturbation of which it has had no previous experience. A species with a low *r*-component may be eliminated if faced with new external perturbations that occur with such rapidity that it does not have sufficient time in which to respond effectively. Conversely, species with a high *r*-component will tend to be relatively low in the hierarchy and have little opportunity to exercise such a *K*-component as they may possess; such species when freed from the regulating effects of grazing or predation may experience difficulty in achieving stability. However, even aquatic algae, in the appropriate conditions free from predation and on a stable substratum, form climax systems recognizable in stromatolites, today mainly observable in hypersaline lagoons in Australia (Golubic 1976) although very common in Precambrian times before the evolution of the grazing animal (Stanley 1973).

It seems that the bell-shaped configuration characteristic of species with a high *K*-component is universal in its manifestation. R. H. Green (1980), investigating the population structure and distribution of the unionid clam, *Anodonta grandis*, in a small Arctic lake in the Mackenzie Delta, could find no specimens under 5 yr and less than 55 mm in length. Presumably, such individuals must exist somewhere in the system but they are exceedingly rare or difficult to find. Similar configurations have been found in deep-sea populations of bivalves (J. A. Hutchings and R. L. Haedrich, in preparation).

It is also apparent that most mammal and bird populations exhibit similar patterns of size distributions, with the great majority of individuals grouped around a modal size value. This feature was probably more pronounced in former days when stocks were less disturbed by man's activities. Such distributions tend to pass unremarked because of the degree of genetic control exercised in the growth pattern of the individual. However, assuming that animals with genetic control of size have evolved from phyla in which it is now lacking, genetic control must have considerable survival value for it to have become incorporated in the hereditary mechanism.

THE CLIMAX

The vegetational climax, as characterized by the virgin forest, has many similarities with the ecosystems developed in Arctic lakes. These similarities are most readily discerned in the structure of the dominant species. In an examination of the characteristics of virgin forests in Europe, Jones (1945) stressed the uniformity of the individuals within stands: "many reports of even-aged stands are doubtless based on appearances only, or at most on stem-diameter

frequencies, which, as will be seen, can be misleading. It is, moreover, impossible to determine the age of an old tree accurately within 15 to 20 years, especially when it has endured in youth all the hardships and misfortunes of a natural environment." Describing a particularly uniform stand of beech, *Fagus sylvatica*, in Bosnia, Jones continues: "Regeneration in such forests often appears to be absent, and there is a striking deficiency of smaller stems, giving a diameter distribution which may approach that of an even-aged stand. This, however, does not mean that the forest is not reproducing itself and maintaining its present structure." In this particular example 70% of the stems were between 170 and 200 yr old, with the youngest tree in the modal size group being 90–100 yr of age.

At Heart's Content Forest Reserve, Pennsylvania, Morey (1936a, 1936b) found that specimens of hemlock, *Tsuga canadensis*, 820 mm in diameter had a very wide range of age: although the mean age was close to 400 yr, only two of three trees were found to be between 359 and 445 yr old.

The relatively small number of stems forming the potential replacement stock has been discussed by Borman and Likens (1979). They pointed out that different species exhibit different nuances within what they term the "advance regeneration strategy." Quoting Forcier (1973, 1975), they stated that many shade-tolerant species such as beech, sugar maple, *Acer saccharum*, and red spruce, *Picea rubens*, are able to maintain, in fairly deep shade, populations of seedlings *whose ages range over several decades*.

The processes determining population structure in these virgin forests appear identical with those in Arctic fish stocks, and the problems of aging and stock dynamics appear to be equally difficult even when all individuals can be counted and measured.

The fundamental difference between the structure of forest and lake ecosystems is that in forests the dominant species is also the primary producer, whereas in a lake the dominant fish species is terminal in the energy flow path. It seems that it is for this reason that Whittaker and Woodwell (1972) found it difficult to apply the climax concept to aquatic ecosystems. The difference between terrestrial and aquatic systems, they stated, is due to the contrast in evolutionary response to a stable surface as provided by the land compared with an unstable suspension in water. It is precisely this feature, combined with the effect of grazing, that prevents stability from developing in aquatic primary producers; fluctuation in primary producers allows, and necessitates, the development of stability at the terminal trophic level, if chaotic fluctuations are to be avoided. If stability cannot be achieved by the primary producers then the opportunity passes along the energy flow path until greatest stability is attained with whatever species are available. Where erratic environmental conditions give rise to terrestrial grasslands, ungulates frequently assume the dominant role, although in the absence of placental mammals, marsupials, as in Australia, or birds, such as the moas of New Zealand, may assume dominance, conferring greatest steadiness on the system. In the forest, fluctuations in leaf production give rise to secondary trophic series that again terminate in species exhibiting maximum stability.

The concept of the climax has passed through a large number of changes and modifications since it was first considered to be a superorganism (or supraorganism) by Clements (1916, 1936). The various views and changes have been reviewed in detail by Whittaker (1951, 1953), Langford and Buell (1969), and Odum (1969, 1971). At the present time there still seems to be little unanimity in view; Borman and Likens (1979) even questioned the conceptual value of the climax, suggesting that change is a more recognizable property of ecosystems than constancy.

The original concept of Clements (1916, 1936), further developed by Phillips (1934, 1935a, 1935b), that the climax can be regarded as a superorganism, or organized functional whole, generally found little support. Gleason (1926, 1939) expressed the diametrically opposed view that the climax represented the sum of the individual characteristics of a fortuitous aggregation of plants as they found expression under the prevailing environmental conditions. Tansley (1935) adopted a somewhat intermediate position; he recognized an underlying degree of order that he found difficult to pinpoint, concluding that an ecosystem could be described as a "quasi-organism" but strongly opposing the idea of any mutualistic interaction between species that might give rise to a "community" or to communal goals. In fact, Tansley rightly opposed the use of the term "community," coining the term "ecosystem" with which to replace it: a message that has subsequently gone almost unheeded; the term "community" is essentially Clementsian in its implications.

The work of Curtis and McIntosh (1951), McIntosh (1967), and Whittaker (1967) tended to support the views of Gleason. Whittaker (1967), for example, demonstrated the independence of individual species in plant associations. Along a complex environmental gradient individual species were found to increase in importance, reach a maximum value, and then decline in abundance as optimum conditions were passed; optimal conditions for each species appeared independent of all others. Langford and Buell (1969) stressed the order and stability of the climax, adopting a position closer to that of Tansley rather than that of Gleason. Drury and Nisbet (1973) effectively questioned many of the assumptions that have grown up around the climax concept, particularly the notion that the climax is a state of maximum biomass accumulation and that organisms in the early stages of succession facilitate the entry and establishment of later arrivals. Jones (1945) concluded that the climax could be variable and illusive, fluid and flexible depending on the local conditions and the past history of the biota at the site in question. Whittaker and Woodwell (1972) concluded that the forest climax is characterized by maximum accumulation of biomass and steady states of species populations, productivity (approximate balance of gross photosynthesis and respiration), and nutrient circulation. The forest community, they stated, has a stability derived from the long-lived dominant species that endows it with a "time-binding" character embodying the historical events provided by past years' environments and species interactions; its characteristics, they believe, can best be described as a loosely ordered steady state.

Order is evident in the structure of the climax, as seen in the regular sequence of events that takes place during succession (Drury and Nisbet 1973; Horn 1975; Pickett 1976; Connell and Slayter 1977). Pickett (1976) stated that succession is a completed gradient of decreasing physical stress through

time. In this context decreasing stress may be defined as a reduction in internal fluctuation of both physical and biological factors; therefore, the system comes to the steadiest state attainable within the prevailing environment and the species available. Given relative constancy in the driving variables of moisture, nutrient, sunshine, and species composition, a greater degree of steadiness will be attained within the well-defined boundaries of an autonomous sytem than in a more open system subject to the exchange of biota through immigration or emigration; as Tansley (1935) pointed out, the greater the autonomy of the system the greater its dynamic stability.

Within an autonomous system the steady state is attained by interaction between the various species; by definition all species are different therefore interaction between them is asymmetrical, resulting in the formation of a hierarchy. At the head of the hierarchy is the dominant species, the one that can develop the best integration of energy acquisition and conservation; this is therefore the species that exhibits least fluctuation and imposes the greatest damping moment on the system as a whole. In view of the long periods of time available, a small advantage will confer great benefit on the dominating species: it is frequently found that approximately 10% of the species in an ecosystem accumulate some 90% of the total biomass (Whittaker 1964; Longhurst and Williams 1976; Longhurst 1980).

The structure and pattern of energy flow through an ecosystem will greatly influence its stability in the face of perturbation by external agents such as the imposition of a fishing regime. Stability in face of external perturbation, i.e. one that alters only the variables of state, not the driving variables (Holling 1973), is characterized by (1) the amplitude of the deflection from the ground state, (2) the rapidity of the response, and (3) the rate at which the deflection is damped (Hurd et al. 1971; Johnson 1981). In biological systems the damping process is greatly influenced by the degree of autonomy of the system. In a small Arctic lake the system can withstand a high degree of displacement through the removal of a large fraction of the fish stock, without impairment of its capacity to recover; recovery is direct and without oscillation, hence manifesting a very efficient damping mechanism. Only in its time to recovery does the system lack one of the essential characteristics of stability; this results from the low energy input and the time required to rebuild the biomass. In general, stability to external perturbations will be achieved where the system is autonomous and the energy pathways are short, broad, and direct, with few alternative routes available to energy transfer; this ensures that energy is transferred directly to the seat of repair.

Ecosystems on the tundra surrounding Arctic lakes are, by contrast, more open, with annual migration of many of their components; they are also internally inhomogeneous. These characteristics allow short-term fluctuation in many of the small animal species, although if populations are not to change with time these fluctuations must be around a mean value, which in itself indicates the existence of an effective damping mechanism. A comparable state of affairs is observable in the ocean systems where the degree of openness is even greater and internal inhomogeneity almost limitless; ultimately, however, the system does have boundaries, in many cases congruent with the boundaries of the biosphere and consequently completely impermeable. Short-term fluctuations are therefore the rule rather than the exception (Longhurst et al. 1972), although when left unperturbed the large marine mammals and fishes impose maximum stability on the system. Lack of impermeable boundaries between the various subsystems allows migration patterns to develop between inhomogeneities in a response to the overall trend toward elimination of the fluctuations causing internal stress.

The climax thus represents an inherently stable state, although one that is fluid and flexible and readily displaced by external or internal perturbation. It is the idealized configuration toward which a given assemblage of species will proceed if it forms an autonomous ecosystem under completely regular energy input. A change in species complement or a departure of the energy regime from complete regularity necessitates a change in the projected climax configuration. In actuality, because of changing inputs and outputs, the climax configuration is attained in relatively few systems; in changing circumstances the general impression is one of change rather than stability. In the absence of long-term environmental changes or the introduction of new species, it represents the "balance of nature" (Egerton 1973): the balance point at which individual species in their integration of energy acquisition and conservation come to the steadiest state attainable in the given conditions. Only if there is universal existence of the homeostatic mechanisms seen so clearly in the single species stocks of fish in Arctic lakes is it possible to understand the continuity and coherence of ecosystems in general. Particularly is this the case in view of the immense perturbations that have been imposed on virtually all ecosystems in recent years: without the existence of inherent damping mechanisms chaotic fluctuations would have developed to a much greater extent than has been the case, as perturbations have been of such magnitude as to render ineffective the functioning of the limit cycles that undoubtedly control the ultimate levels of abundance under steady conditions.

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Symposium on the Fisheries and Oceanography of the Strait of Georgia

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The Strait has become the center of many marine activities, and the management of these activities requires knowledge of the entire Strait of Georgia ecosystem. The first symposium on the Strait of Georgia was organized to obtain a free exchange of ideas among scientists working in the area. Prior to the holding of this symposium, there has never been a time when scientists of different disciplines working in the Strait have been able to get together at one time. The symposium served as a forum for the exchange of ideas on how the physics, biology, and geology of the Strait are associated with such applied problems as fisheries and pollution management. The following papers were invited as reviews of these five topics.

The symposium was hosted by the Fisheries and Oceans Pacific Biological Station and was held in Nanaimo, B.C., February 18 and 19, 1982. In addition to the 6 review papers, 14 contributed papers were also presented in the afternoon sessions and these are published elsewhere, as appropriate. Collectively, the review papers form a "bench mark" from which future progress can be judged; at the same time, many gaps in our knowledge are emphasized where further interdisciplinary research is required.

The symposium was opened on a keynote address given jointly by Dr John O'Riorden, Director, Planning Branch, and Mr Gordon Halsey, Director, Marine Resources Branch, both of the Ministry of the Environment of British Columbia. In his commentary, the latter speaker pleaded with his audience of scientists to make their work relevant to the local scale of issues, which sometimes meant answering a citizen's concerns regarding his particular 10-m stretch of shorefront. The government's concern to the level of a citizen was rightfully expressed, and indeed, among the audience there were persons representing citizens groups (e.g. the Gulf Island Trustees) as well as private individuals. However, on a broader scale of relevance, it is hoped that these background papers will help in the decision-making process for the proper management of one of Canada's most scenic and fascinating environments.

Concern by scientists and managers over the Strait of Georgia is not new, and in fact, comments made almost a century ago show the difficulty of communicating the need to manage the Strait to the private enterprise users. Thomas Mowat (1889) commented with regard to fisheries regulations: "The order limiting the number of boats to 450 for the Fraser was at first unpopular, and excitement among a certain class ran high. But most of this disturbance was created by men who had never been in the fishing business, backed up by a number of aliens..." or again: "The restriction compelling canners to keep the offal from drifting into the water was very difficult to enforce."

Rather later, when Hutchinson and Lucas (1931) undertook what was perhaps the first multidisciplinary oceanographic survey of the Strait, relevance to public interest was the main motivation: "The original problem which gave the primary impetus to the present investigation was the feasibility of diverting the migrations of salmon by closing Canoe Pass..."

A deeper understanding of the physics and biology of the Strait has been possible only through thorough scientific investigation, which is represented here in the reviews presented. The interpretation of much of this work down to the scale requested by Mr Halsey requires individual scientists to participate in public hearings. However, this can sometimes be a source of bewilderment to the scientist, as much as to the public who are trying to understand the science. An example, which I gave at the symposium, was the recent hearings (Comox, B.C., April 7 and 8, 1981) on the Cape Lazo sewage disposal system. At this hearing, an intelligent and vociferous group of island opponents were able to convince the Pollution Control Board members of the dangers of this enterprise using quotations from Pope Leo on the quality of life. Personally, I believe that the scientific evidence should have favored Shakespeare (*Twelfth Night*, Act I, Scene 1): "Nature with a beautious wall doth oft close in pollution..." The final acts in the Strait of Georgia management drama may never be written, but we hope as scientists to be informative in having invited public participation and newspaper coverage in this our first symposium on the Strait of Georgia.

In conclusion, I would like to express my sincerest thanks to the symposium steering committee consisting of Dr C. D. Levings, Dr R. E. Thomson, and Mr A. J. Dodimead, all of the Department of Fisheries and Oceans. My thanks also go to Mr Wayne Shinners and Dr Richard Beamish who hosted the meeting.

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Substrates of the Strait of Georgia, British Columbia[1]

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LUTERNAUER, J. L., J. J. CLAGUE, AND C. H. PHARO. 1983. Substrates of the Strait of Georgia, British Columbia. Can. J. Fish. Aquat. Sci. 40: 1026 – 1032.

The subtidal floor of the Strait of Georgia west of the Fraser River Delta and north to Texada Island is blanketed mainly by silt and clay derived from the Fraser River and from failed deposits at the delta front. On the western part of the Strait south of the delta to the San Juan and Orcas islands, sediments are mainly lag sand and gravel eroded from Pleistocene deposits by strong tidal currents. East of this area in a more sheltered embayed part of the Strait the seafloor is covered by silt and clay derived from local mainland streams and possibly from the Fraser River. North of southern Texada Island, influence of the Fraser River also has been minimal. Although bottoms of basins in this part of the Strait are blanketed by mud, coarser sediments are dominant elsewhere. Substrate materials in the northern Strait are products of wave and current reworking of Pleistocene deposits and deposition from local streams and rivers. The shoreline of the Strait is mainly rocky but includes sand and/or gravel beaches and deltaic tidal flats. Development of the intertidal zone has been controlled by Pleistocene glaciation, postglacial changes in sea level, local wave and current regimes, and sediment availability.

LUTERNAUER, J. L., J. J. CLAGUE, AND C. H. PHARO. 1983. Substrates of the Strait of Georgia, British Columbia. Can. J. Fish. Aquat. Sci. 40: 1026 – 1032.

Le plancher subtidal du détroit de Géorgie à l'ouest du delta du fleuve Fraser et vers le nord jusqu'à l'île Texada est recouvert en grande partie de vase et d'argile provenant du fleuve Fraser et de dépôts disloqués au front du delta. Dans la partie occidentale du détroit au sud du delta et jusqu'aux îles San Juan et Orcas, les sédiments sont constitués surtout par des résidus de sable et de gravier, produits de l'érosion des dépôts du Pléistocène par de forts courants de marée. À l'est de cette zone, dans une partie échancrée plus abritée du détroit, le fond est recouvert de vase et d'argile provenant des cours d'eau de la terre ferme et possiblement du fleuve Fraser. Au nord de la portion méridionale de l'île Texada, l'influence du fleuve Fraser a été minimale. Bien que dans cette partie du détroit, le fond des bassins soit recouvert de vase, ailleurs, des sédiments plus grossiers dominent. Dans la partie septentrionale du détroit, les matériaux du substrat sont le produit de l'érosion des dépôts du Pléistocène par les vagues et les courants, et la déposition en provenance des cours d'eau locaux. La ligne de rivage du détroit est en grande partie rocheuse, mais comprend des plages de sable ou de gravier, ou des deux, et des veys deltaïques. La formation de la zone intertidale a été réglée par la glaciation du Pléistocène, les changements postglaciaires du niveau de la mer, les régimes de vagues et de courants locaux et enfin la présence de sédiments.

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THE Strait of Georgia (Fig. 1) is part of a structural depression that has subsided intermittently since Late Cretaceous time, in response to subduction along the British Columbia continental margin (Atwater 1970; Mathews et al. 1970; Mathews 1972; Riddihough and Hyndman 1976; Muller 1977; Riddihough 1977, 1979; Roddick et al. 1979; Rogers 1979). Upper

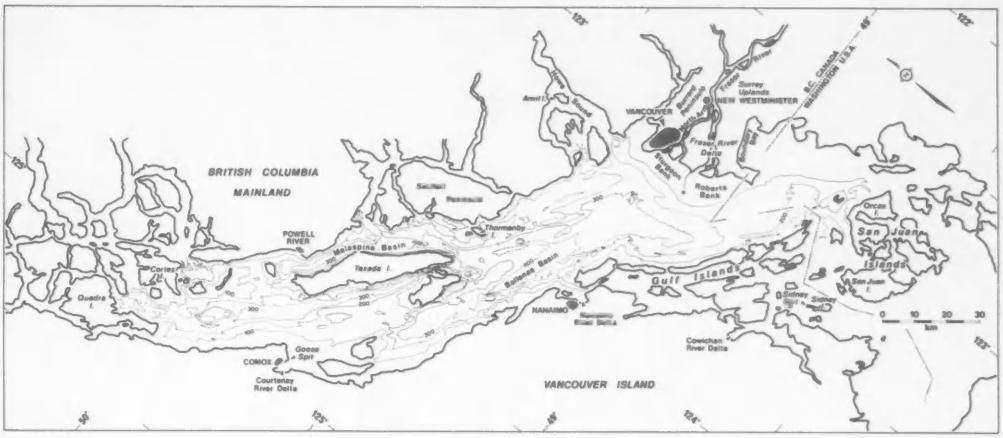

FIG. 1. General bathymetry and geographic locations, Strait of Georgia. Contours in metres.

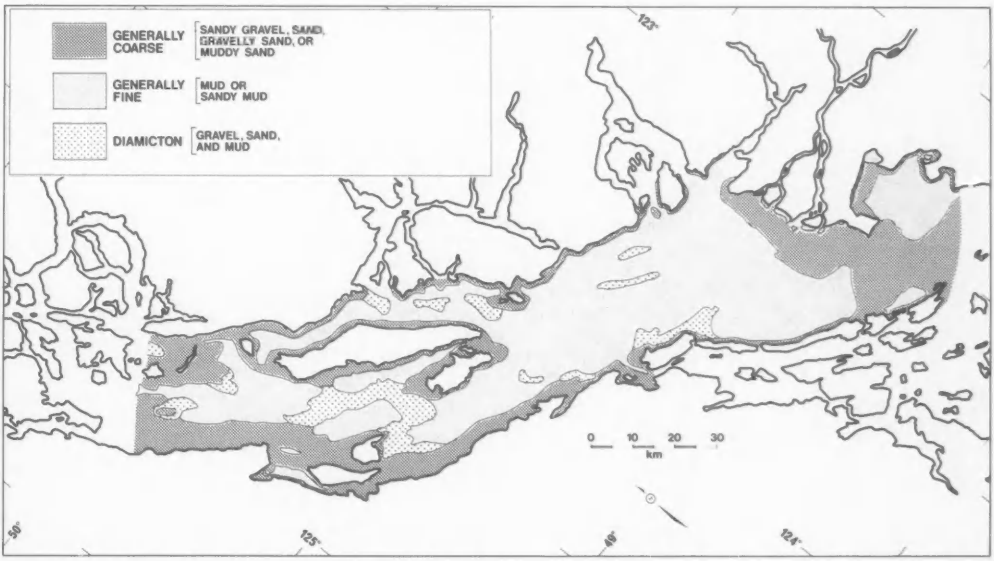

FIG. 2. Subtidal substrate distribution in the Strait of Georgia.

Cretaceous and Tertiary sediments that accumulated in this depression have been buried by Pleistocene and postglacial detritus (Tiffin 1969; Clague 1976, 1977; Pharo and Barnes 1976; Luternauer 1980; Clague and Luternauer 1982). The physiography of the Strait primarily reflects (1) sculpting of Pleistocene deposits and bedrock by glaciers, the last of which occupied the depression from about 25 000 to 12 000 yr ago (Tiffin 1969; Clague 1976), and (2) deposition from the Fraser River.

Sedimentology of Subtidal Substrates

SUBSTRATE DISTRIBUTION

Substrates south of the Fraser River Delta in the western part of the Strait of Georgia are mainly sand and gravel (Fig. 2) (Pharo 1972; Pharo and Barnes 1976; Luternauer 1976, 1980). The gravel is well washed and encrusted with molluscs, brachiopods, bryozoans, and worm tubes. These

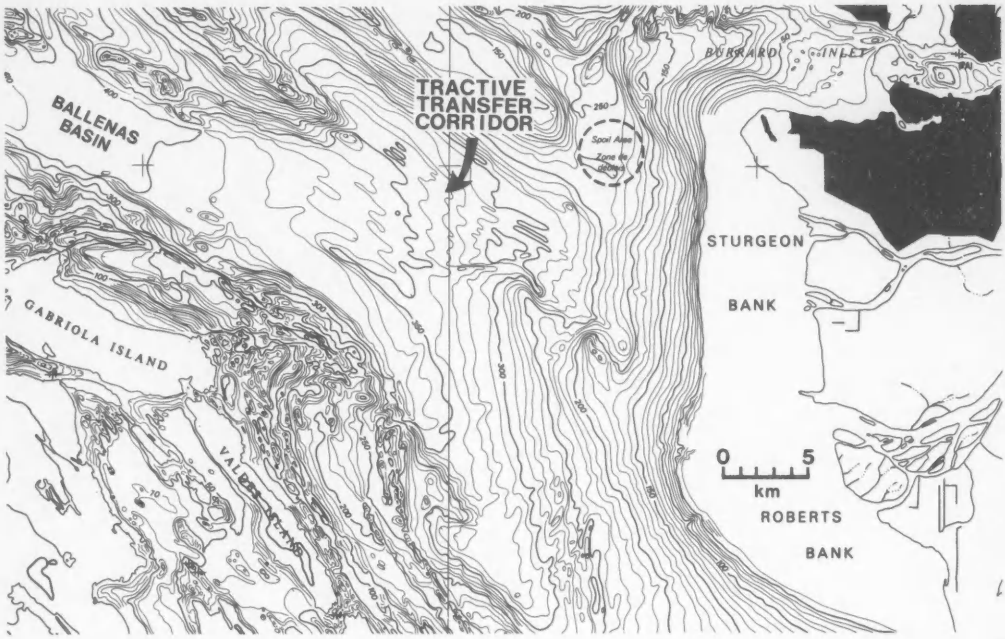

FIG. 3. Detailed bathymetry of southcentral Strait of Georgia. Contours in metres. (Base map: Canadian Hydrographic Service Natural Resource Map 15792-A.)

coarser sediments gradually fine towards the east, and in the vicinity of Boundary Bay sandy mud and mud (silt and clay) are dominant (Pharo 1972; Pharo and Barnes 1976). In the central Strait west of the Fraser Delta and northwest to southern Texada Island, mud blankets most of the sea floor. Silt is the main component in the southern half of this area and clay in the northern half (Pharo 1972; Pharo and Barnes 1976). Patches of diamicton (mixed mud, sand, and gravel) commonly associated with sponges are present in the central Strait adjacent to parts of the Vancouver Island coast and on ridge tops (Pharo 1972). In the northern half of the Strait of Georgia from Texada Island to Quadra and Cortez islands mud substrate is dominant only in deep basins and troughs, a band of sand and gravel adjacent to the coast broadens progressively towards the north, and patches of diamicton are widespread (Clague 1977).

SEDIMENTATION IN THE CENTRAL STRAIT OF GEORGIA

Formation of the Fraser River Delta — About 10 000 yr ago, after the last Pleistocene glaciers had disappeared from British Columbia, the Fraser River began to empty into the Strait of Georgia through a gap in the Pleistocene uplands at New Westminster and built a delta to the south and west (Clague and Luternauer 1982). By about 8000 yr ago, when the sea in this area stood 12 m or more below its present level with respect to the land (Mathews et al. 1970; Clague et al. 1982), an intertidal platform probably extended far to the southwest of New Westminster. A marine transgression that followed from about 7500 to 5500 yr ago inundated parts of the earlier formed delta and temporarily inhibited its seaward advance. Sea level stabilized within a metre or two of its present position about 5500 yr ago, whereupon a substantial area of the delta became emergent and large bogs began to form (Hebda 1977; Clague and Luternauer 1982). Most or all of the southern delta front at Boundary Bay already was in existence at that time (Kellerhals and Murray 1969). During the last 5000 yr, the Fraser Delta has grown westward into the Strait of Georgia under conditions of comparatively stable sea levels. Fraser River flow across the Delta during this period has been concentrated along the present main distributary channel and along the north edge of the delta (Mathews and Shepard 1962).

Dispersal of Fraser River suspended matter — During the freshet period (May–July) the sediment-charged plume from the Main Channel of the Fraser River extends far into the Strait of Georgia. Several mechanisms drive suspended sediment preferentially northward from the Main Channel mouth at Sand Heads. The Coriolis effect acts in concert with tidal drag to deflect the plume towards the Sturgeon Bank slope on a flooding tide. On an ebbing tide more fine sediment can be directed to the north than south because the southeasterly ebb tidal drag on the plume can be balanced by the Coriolis effect (Thomson 1981) and because surface water adjacent to Sturgeon Bank appears to flow northward persistently during

the summer, regardless of tidal phase (Giovando and Tabata 1970; Tabata et al. 1971; Tabata 1972; Luternauer and Murray 1973; Luternauer 1980). The northward residual surface current on the eastern side of the Strait (Thomson 1981) transports suspended Fraser River detritus into Howe Sound as far as Anvil Island (Syvitski and Macdonald 1982) and up to Sechelt Peninsula. Some sediment in surface waters that reaches the western side of the Strait may be carried back to the east by an intermittent clockwise eddy (Tabata et al. 1971) and, hence, also be entrained in the northward flow.

Silt-size particles discharged by the Fraser River are mostly blocky, equant to subequant grains of quartz, feldspar, and subordinate rock fragments and other minerals, which settle slowly but continuously through the water. Clay-size particles and the platy clay minerals and micas settle even more slowly and are carried farther north (Pharo 1972; Pharo and Barnes 1976). The silt and clay have accumulated more thickly in the basins of the central Strait than on ridges (Tiffin 1969; Pharo and Barnes 1976). Diamicton deposits in the central Strait are probably Pleistocene glacial deposits that have been partly reworked by tidal currents and veneered by fine sediment from the Fraser River.

Tractive transfer off the Fraser River Delta slope — Gullying of the Fraser River Delta slope probably is initiated principally by failure of oversteepened deposits at a channel mouth (Luternauer 1980; Luternauer and Finn 1983). Mechanisms that may help maintain the gullies are the intermittent sliding of accumulated gully bottom sediments and the flushing action of tidal currents (Shepard and Milliman 1978; Luternauer 1980). The many submarine channels at the centre of the Strait off the northern part of the delta front (Fig. 3) suggest that this area has been a major corridor for tractive transfer (by such mechanisms as turbidity and density currents) of sediments derived from the Sturgeon Bank slope and deposited in Ballenas Basin. This process probably persisted until relatively recently, for the channels on the sea floor are well defined, and acoustic reflectors (presumably turbidites) recur throughout much of the upper postglacial deposits in Ballenas Basin (Tiffin 1969). However, today, Sturgeon Bank slope is blanketed by mud (Luternauer 1976, 1980) and lacks gullies that extend into the tractive transfer corridor, suggesting that major tractive flows no longer occur there (Luternauer and Finn 1983). The channels on the floor of the Strait thus may be relict features (somewhat masked by younger sediments deposited out of suspension) that formed when river discharge was more highly concentrated along the north edge of the Delta. Today, tractive flows probably are common only in the gullies of the Main Channel.

Sedimentation South of the Fraser River Delta and in the Northern Strait

The dominant northerly transport direction of suspended sediment and tractive flows has left much of the western Strait south of the Main Channel mouth at Sand Heads sediment starved. The meager supply and sediment coupled with high tidal currents (Pickard 1956; Tiffin 1969; Pharo and Barnes 1976; Luternauer et al. 1978; Luternauer 1980) has led to the formation of sand and gravel lag deposits from Pleistocene glacial drift. To the east, these sediments grade into silt and clay that have been derived from local mainland rivers and possibly from the Fraser River.

In addition to coarse sediments being more widespread in the northern Strait than in the central Strait, fine postglacial sediments are not as thick as in the central Strait (Tiffin 1969; Clague 1977) (Table 1). This evidence suggests that (1) tractive flows from the Fraser River Delta have not carried material much beyond southern Malaspina Basin and the constriction at the northwestern end of Ballenas Basin and (2) little suspended sediment in the Fraser River plume is carried beyond Texada Island. Thus, most of the substrate materials in the northern Strait are of local origin; some have been eroded from coastal bluffs and seafloor Pleistocene deposits, and others have been introduced from inland deposits by adjacent rivers.

Nature and Origin of Intertidal Substrates

The shorezone of the Strait of Georgia comprises rocky shorelines, beaches, and deltas (Fig. 4) (Bornhold et al. 1979; Clague and Bornhold 1980; Luternauer 1980; Owens 1980; Dunn 1981; Swinbanks and Murray 1981; Hale and McCann 1982). Beaches are best developed adjacent to lowlands underlain by thick unconsolidated sediments as, for example, along much of eastern Vancouver Island and in the vicinity of Powell River and Vancouver. In these areas, fairly broad intertidal and shallow subtidal platforms eroded on Pleistocene sediments extend seaward from the present shoreline. These platforms have formed during postglacial time by landward retreat of the coast, caused in part by a relative sea level rise of at least 12 m during the last 7500 yr. Some shallow banks in the Strait of Georgia also may have been leveled by waves during this period.

The intertidal platforms are generally covered by thin sand and gravel regularly moved by waves and/or currents (Hale and McCann 1982) and by boulders that are immobile even during the most severe storms. Beaches bordering the Strait of Georgia are subject to seasonal changes in morphology due to varying directions and strengths of winds and waves (Harper 1980). On more exposed beaches, sediment may be eroded and moved offshore during winter when wave energy is high. Accretion can occur on these beaches during summer when sediment is more likely to be moved shoreward by lower waves. On more sheltered beaches where fetch is restricted, reversals in the direction of littoral currents caused by seasonal changes in wind direction may be more significant than winter–summer differences in wave energy in causing erosion–accretion patterns. In these areas, storms erode material from one area to deposit it again at a downdrift location; thus, erosion and accretion may occur on the same beach at the same time. Where drift is dominantly in one direction, spits, bars, and broad banks are developed downcurrent from eroding cliffs. Examples in the Strait of Georgia include Goose Spit near Comox and Sidney Spit on Sidney Island (Clague and Bornhold 1980).

A major portion of the Strait of Georgia shoreline, including much of the coast of southern Vancouver Island, the mainland north of the Fraser Delta, and most islands, is rocky. The intertidal zone in these areas, which in general is narrow, irregular, and drops off over a short distance into deep water,

TABLE 1. Estimated postglacial sedimentation rates in various parts of the Strait of Georgia.

Area	Vertical rate (cm/yr)	Significance	Method	Source
Fraser Delta front				
Off Main Channel				
At 37-m depth	34 (460 horizontal)	Average	Displacement of bathymetric contours between 1929 and 1959	Mathews and Shepard 1962
At 90-m depth	37 (850 horizontal)	Average		
At North Arm mouth area	0.1	Average over last 6600 yr	Radiocarbon	This report
Roberts Bank slope				
Central at 60-m depth	0.2 (0.5)	Average over last 800 yr; average corrected (parentheses) for radiocarbon "reservoir age" determined from shell of living organism	Radiocarbon	This report
Southern at 20-m depth	0.5 (3.0)	Average over last 500 yr; average corrected (parentheses) for reservoir age	Radiocarbon	This report
Central and northern Strait				
Central Strait				
Off Fraser Delta	2.7	Maximum over 10 000 yr	Seismic profile	Mathews and Murray 1966
Northern part of basins	0.6	Average over 10 000 yr	Seismic profile	Mathews and Murray 1966
Ballenas Basin	2.0	Average over 10 000 yr	Seismic profile	Tiffin 1969
Ballenas Basin	2.6	Maximum over 10 000 yr	Seismic profile	Tiffin 1969
Southern Malaspina Basin (in the source reference the basin is assumed to extend to the area off Thormanby Island)	2.3	Maximum over 10 000 yr	Seismic profile	Tiffin 1969
Northern Strait				
Entire area	0.1	Average over 12 500 yr	Seismic profile	Clague 1977
Basins	1.4	Maximum over 12 500 yr	Seismic profile	Clague 1977

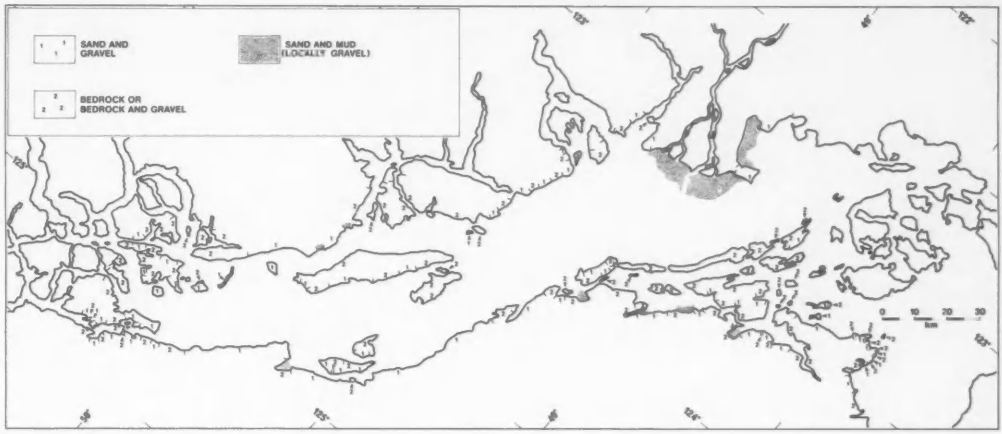

FIG. 4. Intertidal substrate distribution in the Strait of Georgia.

was sculpted mainly by glacial erosion. Most rock-dominated coastal areas contain small pocket beaches covered by gravel.

A relatively small portion of the Strait of Georgia coastline is deltaic. The largest delta, of course, is that of the Fraser River, but there are numerous smaller ones at the mouth of the Nanaimo, Cowichan, Courtenay, and several other rivers. Most deltas in the Strait are currently growing because deposition of sediment by rivers exceeds erosion by waves and currents. Dredging and training of these rivers and erection of jetties and causeways across tidal flats can, however, influence the rate and pattern of delta growth (Luternauer 1980).

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The Strait of Georgia: functional anatomy of a coastal sea[1]

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LEBLOND, P. H. 1983. The Strait of Georgia: functional anatomy of a coastal sea. Can. J. Fish. Aquat. Sci. 40: 1033–1063.

The physical oceanography of the Strait of Georgia, a large estuary on the coast of British Columbia, is reviewed in the light of recent observations and theoretical developments. The review focusses on a discussion of physical mechanisms rather than on a description of properties. The responses of the Strait to the dominant forcing processes, the tides, freshwater runoff, and atmospheric inputs, are described first. Interactions between these responses are then shown to give rise (or at least to influence) other phenomena such as fronts, deepwater renewal, and oceanic exchange processes. Recent observations of deep residual flows as well as theoretical efforts to explain their nature are also discussed. The present state of the understanding of dynamics is assessed against the requirements of predictive modeling; whereas high-frequency phenomena such as tides and upper layer dynamics are approaching an engineering level of predictability, low-frequency processes (water renewal, oceanic exchange, deep residual flows) remain inadequately documented, poorly understood, and unpredictable. Some suggestions are presented for future observational and theoretical research.

LEBLOND, P. H. 1983. The Strait of Georgia: functional anatomy of a coastal sea. Can. J. Fish. Aquat. Sci. 40: 1033–1063.

Le présent article est une revue de l'océanographie physique du détroit de Géorgie, un grand estuaire de la côte de la Colombie-Britannique, à la lumière de récentes observations et de développements théoriques. On met l'accent sur un examen des mécanismes physiques plutôt qu'une description de propriétés. On décrit tout d'abord les réponses du détroit aux forces dominantes : les marées, les arrivées d'eau douce et les apports atmosphériques. On démontre ensuite que les interactions entre ces réponses produisent, ou tout au moins influencent, d'autres phénomènes, tels que fronts, renouvellement des eaux profondes et processus d'échanges océaniques. On analyse également les récentes observations des flux résiduaires profonds ainsi que les considérations théoriques pour en expliquer la nature. Notre compréhension actuelle de la dynamique est évaluée en rapport avec les exigences d'une modélisation prévisionnelle; alors que les phénomènes qui surviennent fréquemment, tels que les marées et la dynamique des couches supérieures, peuvent être prédits avec une précision approchant les niveaux requis pour les travaux de génie, les processus moins fréquents (renouvellement de l'eau, échanges océaniques, flux résiduaires profonds) sont inadéquatement documentés, mal compris et imprévisibles. Quelques suggestions sont offertes pour observations et recherches théoriques futures.

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REVIEWS of the physical oceanography of the Strait of Georgia were presented about 50 and 25 yr ago, respectively, by Hutchinson and Lucas (1931) and Waldichuk (1957). These reviews presented extensive discussions of the observations then available as well as much of the actual data. There has been enormous progress and expansion of oceanography in this past 25 yr, and this review cannot possibly follow the format of its predecessors. Progress (Stewart 1980 has called it a "revolution") has come about through the development of new systems of compact in situ sensors, accompanied by the growth of digital computing machines and techniques for the presentation and analysis of information. Rapid, high-resolution sampling has revealed hitherto unsuspected oceanic features and brought with it a profound reevaluation of many of the foundations of physical oceanography; it has also produced a mass of data more suited to presentation in an atlas than in a review paper.

In keeping with a modern view of physical oceanography, which emphasizes the study of mechanisms rather than the description of properties, this review will present various kinds of circulation and scales of motion that coexist in a coastal sea such as the Strait of Georgia and discuss their

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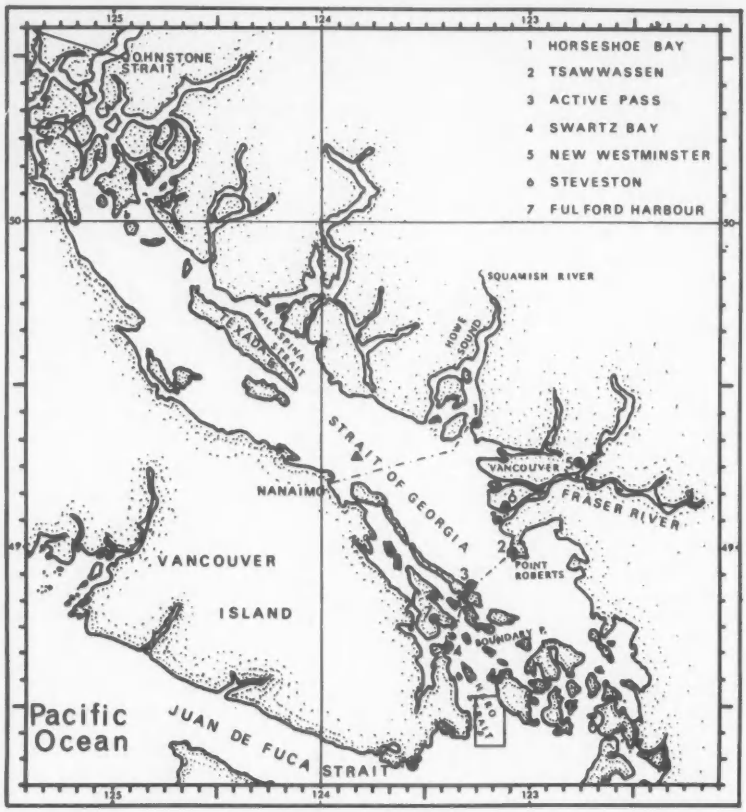


FIG. 1. The Strait of Georgia and its accesses to the Pacific Ocean. Johnstone Strait is off the map to the northeast; the Gulf and San Juan islands lie between the Strait of Georgia and the Strait of Juan de Fuca. Ferry crossing routes mentioned in the text are shown as broken lines. The triangle in the middle of the Strait of Georgia shows the position of the data shown in Fig. 14. The rectangle enclosing the southern part of Haro Strait delineates the area shown in Fig. 4.

interactions. References to recent observational and interpretative works will be extensive but not comprehensive. An exhaustive survey of the oceanographic data collected in Strait of Georgia waters has recently been compiled by D. D. Lemon and D. M. Kowalski (Arctic Sciences Ltd., Sidney, B.C., unpublished manuscript).

A general and extremely well-illustrated review of the physical oceanography of the coast of British Columbia has also been presented by Thomson (1981); this book describes many oceanographic features of the Strait of Georgia.

The Strait of Georgia is fringed by a number of tributary inlets, bays, and sounds, some of which are shown in Fig. 1. Most of these have been extensively surveyed (Pickard 1961, 1963, 1975; Herlinveaux 1962; Lazier 1963; Davidson 1979) and their study has contributed to the general knowledge of estuarine dynamics. Most of the inlets have shallow sills and no direct deepwater connection with the Strait of Georgia; they all contribute small amounts of runoff compared with the Fraser River. I will therefore assume that the dynamics of the inlets are not significantly coupled back to those of the Strait and for that reason as well as out of consideration of the space available will not discuss them further.

Some of the physical oceanographic research performed in the waters of the Strait of Georgia has been concerned with problems of universal rather than local relevance: studies of air–sea interaction (Stewart 1969; Elliott 1972), surface wave generation (Garrett 1969; Dobson 1971), and microstructure (Bilodeau 1978). Investigations of the internal waves ubiquitous in the surface layer of the Strait (Gargett 1976; Gargett and Hughes 1972; Samuels and LeBlond 1977) as well as the development of remote sensing techniques and their application to the Strait of Georgia (Gower and Oliver 1979; Aranuvachapun and LeBlond 1981) also transcend the bounds of this local review and will be mentioned only inasmuch as they shed light on the dynamics of the system.

I have organized the review as follows. In the first section,

the development of conceptual models of the physical oceanography of the Strait of Georgia from the more geographical early approach to the current interpretation in terms of coupled dynamic systems is traced. Subsequently, the causally dominant parts of this complex fluid engine, the tides and the estuarine circulation, are then surveyed followed by a description of the role of atmospheric inputs. Fronts and deepwater renewal are discussed; these are viewed as complex interactions between the tides and the estuarine system. The fundamental questions raised by observations of deep residual flows are discussed, followed by consideration of exchange with the Pacific Ocean. The possibility of predictive modeling of the Strait of Georgia as a complex geophysical fluid system is debated; the practical requirements of successful modeling clearly bring out the main gaps in our understanding of the physics! Finally, I present some suggestions for future research.

An Intricate Fluid Engine

The development of physical oceanography has followed closely that of sampling instruments and analysis techniques. The description of the oceanography of the Strait of Georgia has thus grown in scope and in refinement over the years, keeping step with the development of scientific techniques. Hutchinson and Lucas (1931) had a single sampling bottle to work with; their description remained coarse and limited to the upper layer. Waldichuk (1957) reviewed material collected with the most complicated mechanical samplers of classical oceanography: reversing thermometers, sampling bottles, Ekman current meters, and bathythermographs. These were operated from ships for relatively short sampling durations and analyzed mechanically or graphically. The resulting representation of ocean dynamics and of property distributions was strongly conditioned by sampling methods. In coastal as well as in oceanic settings, relatively coarse and brief sampling led to a smooth representation of water properties. The wide spacing of hydrographic stations required for accurate estimation of baroclinic pressure gradients could not reveal complexity on a small horizontal scale; bottles could only be spaced so far apart in the vertical. It must of course have been obvious, even to the investigators of 50 yr ago, that there was much structure in both space and time that was beyond their sampling capacity. Fronts, for example, were just as evident then as they are now, and we still have not made much progress in unravelling their structure. However, the prevailing low sampling resolution, the lack of documentation of the temporal structure, and the relative primitiveness of the theoretical framework conspired to create what I would call a "geographical" view of oceanography. Most simply stated, this point of view assumes that there exist meaningful long-term averages, perhaps slowly varying, of currents and property distributions on which high-frequency phenomena such as waves, fronts, and tides are transient features, like players moving against a stage background. This is of course an oversimplification, but it does sum up my first impression of classical oceanography after reading *The Oceans* (Sverdrup et al. 1942) as an undergraduate.

The gradual development of new instruments (cf. Baker 1981 for an excellent review) has revealed a variability in ocean properties that encompasses the longest time scales; Monin et al. (1977) surveyed the wealth of recently discovered oceanic variability. What is most interesting about the low-frequency fluctuations is not that they are there, for no geophysicist would expect complete steadiness at any time scale, but that they are so strong. Observations in the open ocean (MODE Group 1978) as well as in enclosed seas (Chang et al. 1976) have shown repeatedly that the variance of currents often greatly exceeds the mean, even after filtering out the obvious energetic high-frequency motions such as the tides. Spectra of horizontal current fluctuations are often "red," with increasing energy content at lower frequencies, so that slower "background" fluctuations are more energetic than the faster ones superimposed upon them. In our theatrical analogy, this means that the sets change rapidly and radically enough that a specification of the play rests as much on a description of the low-frequency background as on knowledge of the players' high-frequency actions. There are immediate consequences to the redness of the spectrum. For example, what is now the significance of the term "mean circulation" and how long must one sample to estimate it with some reliability? Flierl and McWilliams (1977) addressed this question, using North Atlantic data, and found that "precise estimates (10% accuracy) may require prohibitively lengthy experiments" with time scales of many years! While no time series of sufficient duration are available in the Strait of Georgia to judge whether these conclusions apply there, a simple example clearly shows the effect of long-term variability on the estimate of "mean" flows.

In a region of strong and variable tides, such as the Strait of Georgia, it has been a frequent practice to estimate the net residual flow at a point as the average of the tidal current over a fortnightly cycle; this type of calculation might then be used to estimate flushing rates or pollutant transport. The progressive vector diagram shown in Fig. 2, drawn from one of the first long-term moorings in the Strait, illustrates the variability of the fortnightly residuals themselves: although there is a net northward trend to the flow over the 50-d sampling period, successive 15-d samples give quite different residual flow vectors. It would then be quite naive to expect that any single 15-d sample would provide a stable estimate of the mean flow over that period. One should then treat with great care earlier estimates of mean flow based on short samples or occasional measurements as, for example, the counterclockwise circulation reported to exist in the Strait of Georgia (Waldichuk 1957).

In addition to having forced upon oceanographers a new view of the marine environment, a view which I call "geological," — longer term events always bring greater changes than short-term phenomena — the strength of low-frequency variability has caused a reassessment of the importance of linkages between various time scales. Theoretical studies of the stability of mean flows and of the nonlinear interactions between fluctuations have shown that the mean can transform itself into fluctuations and vice versa (Robinson and McWilliams 1974; Rhines 1977). In other words, long-period variations are not solely associated with similarly slowly varying causes; they can arise out of rectification of high-frequency events. Conversely, the mean may disintegrate into eddies. The background is not independent of the fluctuations

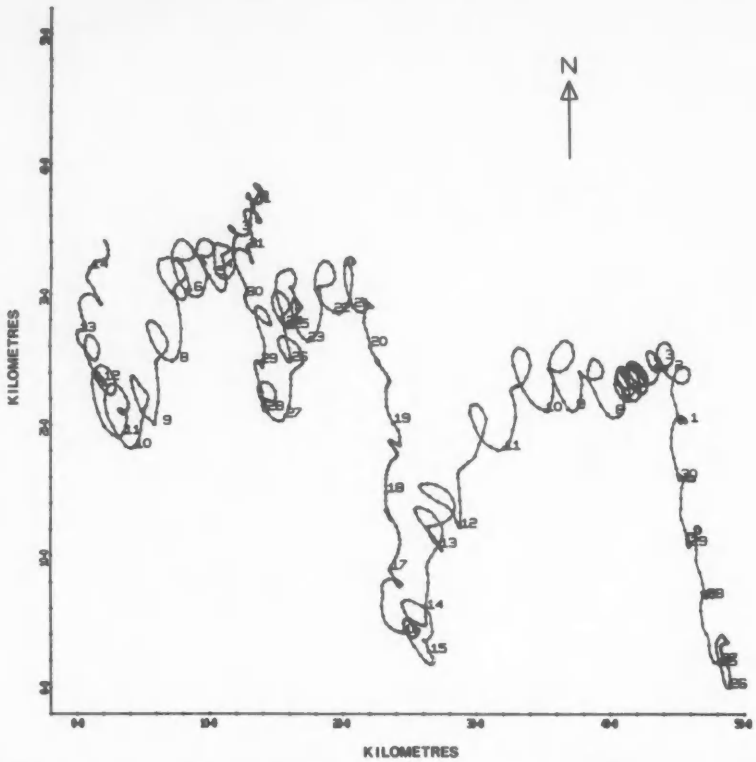


FIG. 2. Progressive vector diagram of horizontal currents measured at a depth of 200 m at mooring H-06 (cf. Fig. 18 for location) from 25 November 1969 (16:42) to 14 January 1970 (09:30). The record begins in the lower right-hand corner (dates 23 and 25 are nearly superimposed). (From Tabata and Stickland 1972a)

and vice versa; on the stage, the scene shifts with the actor's moods, which in turn adapt to the set.

The coupling between various scales suggests that mere superposition is not an adequate conceptual framework to view the behavior of complex fluid systems such as the oceans or, more specifically, the Strait of Georgia. I prefer to think of the physical oceanographic environment of the Strait as an intricate machine, significantly constrained in its behavior by its geometrical configuration and capable of structuring itself through its nonlinear response to inputs of mass, momentum, and energy over a wide range of temporal and spatial scales. One can identify within the machine various systems associated with forcing at specific frequencies (such as the tides) or by particular types of inputs (such as freshwater runoff or solar radiation). Each part of the clockwork is, however, coupled to others so that although parts of the response can clearly be traced to external sources, there are important internal features that are run via nonlinear interactions between the directly forced systems. The important point to remember is that although analogies may be very helpful in clarifying the considerable complexity expected here, they cannot replace the equations of fluid dynamics. The methods of geophysical fluid dynamics are certainly the best and probably the only means of unraveling the interactions between the various systems of our fluid machine. To yield fruitful results they must, however, be used with discrimination and be based on the best available data and qualitative understanding of the environment. It is my hope, then, that this review of the principal systems of motion of the Strait of Georgia will, in addition to being informative to all oceanographers, stimulate specialists into tackling some of the unresolved dynamical problems.

The Tides

The tide consists of sea level variations and associated currents caused by small gravitational imbalances of astronomical origin due to the sun and the moon. These forces are well understood and can be calculated with great precision (e.g. Munk and Cartwright 1966). In small semienclosed seas, the direct effect of the tidal forces is masked by the

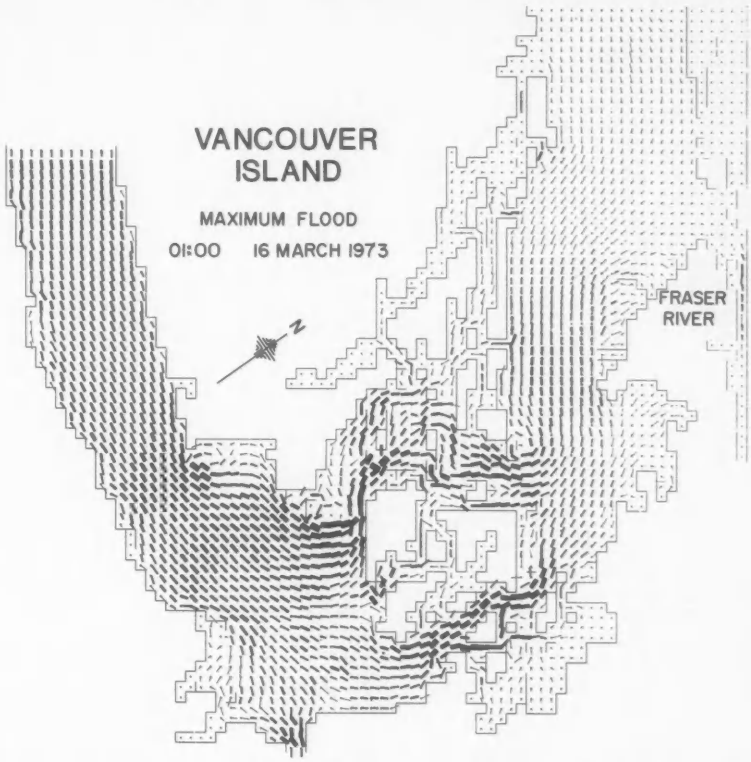


FIG. 3. Tidal currents at maximum flood in the southern Strait of Georgia and Juan de Fuca Strait calculated on a 2-km grid numerical model. Velocity vectors emanate (at small crosses) from the center of each 2-km square. The length of the vector at each point (folded over in parallel segments whenever the speed exceeds 30 $cm \cdot s^{-1}$) gives the flow speed. (From Crean 1978)

response of the smaller basin, which is then said to be cooscillating, to the tides of the larger ocean. The tides of the Strait of Georgia are forced by those of the nearby Pacific Ocean; the progression of the principal tidal constituents along the British Columbia coast and into the Strait through its southern and northern openings has been described by Godin (1980). A thorough description of the tides in the Strait of Georgia and adjacent waters, based on the analysis of tide gauge and current measurements data, has been presented by Parker (1977). Only a cursory sketch is attempted here.

The influence of Pacific Ocean tides reaches the Strait of Georgia through both of its openings: Johnstone Strait to the north and Juan de Fuca Strait in the south. Because of the relatively small cross-sectional area of the northern passages, sea level variations inside the Strait of Georgia are mostly due to inflow via the channels through the Gulf and San Juan islands in the south. Both diurnal and semidiurnal tidal constituents advance through Juan de Fuca Strait as freely propagating waves; frictional effects in the Gulf Island channels significantly retard and damp the tide. Inside the Strait of Georgia proper, phase changes are small and the tide nearly behaves as a standing wave. The character of the tide is mixed, mainly semidiurnal through the whole system, except in the eastern end of Juan de Fuca Strait, where the semidiurnal tidal amplitude is smaller and the tides are still of mixed type but mainly diurnal. Tidal ranges are of the order of 4 m within the Strait of Georgia; tidal currents generally do not exceed 1.0 $m \cdot s^{-1}$, except near and within the narrow and shallow passages leading into the Strait where variable tidal rapids occur, with maximum flood and ebb flows up to 5 $m \cdot s^{-1}$. Tidal currents and sea level changes are the most obvious oceanographic phenomena; they are also the only ones that can be predicted with any reliability.

Tidal predictions are made on a routine basis, using the harmonic method (Foreman 1977), without appeal to an understanding of the hydrodynamics of the ocean waters. Future sea levels and currents at selected points are forecast, to a level of accuracy acceptable for navigation and shore prediction purposes, merely by extrapolating in time a best fit to past observations based on a superposition of signals at the

precisely known tidal frequencies. Since tidal sea level variations and tidal currents dominate the gravitational potential energy and horizontal kinetic energy variances, respectively, routine tidal prediction can provide a description of the major oceanographic variability at any selected point. This threshold of achievement is now so firmly behind us that it is easy to forget its significance!

Tidal prediction by the harmonic method requires the gathering of at least a month of data at the point of interest. Clearly, one cannot sample every point along the shores of our coastal sea, and extrapolation is necessary between data points. Tidal sea level varies spatially on the scale of the external Rossby radius (cf. LeBlond and Mysak 1978, p. 212): $\sqrt{gH}/f$, in standard notation, (where g = acceleration of gravity, H = water depth, and f = Coriolis parameter). In the Strait of Georgia, with an average depth H of the order of 150 m, this scale is of the order of 400 km. Extrapolation for sea level is thus straightforward, since it varies on a scale greater than that of the basin itself; difficulties may be encountered, however, in regions of strong friction or nonlinearity, where the scale may be much shorter. Currents, on the other hand, vary spatially on the scale of the bathymetry as the tide flows through narrow passages or over banks and troughs. The only reliable extrapolation method for tidal currents requires simultaneous knowledge of sea level and proceeds by integration of the hydrodynamic equations.

Numerical tidal models must have been developed for just about every sea of the world by now (cf. Hendershott 1977 for a recent review). With a minor amount of tuning, mainly by adjusting friction parameters, numerical models driven by astronomical tidal forces or, for a marginal sea, by the tides of the nearby ocean can reproduce observed sea level variations with an accuracy equal to that achieved by the harmonic method. The advantage is that both elevations and currents are obtained at every point of a grid tessellating the area of interest rather than only at selected data points. Numerical tidal models of the Strait of Georgia have been developed by Crean (1976, 1978) in a succession of ever-more-refined versions that provide tidal currents and elevations on a 4-km scale over the whole Strait and on a 2-km scale for selected areas. An example of the type of current map provided by Crean's model is shown in Fig. 3. This kind of information has made possible the preparation of maps of current strength, soon to be issued by the Canadian Hydrographic Service. Detailed tidal current information also provides the background for a number of other oceanographic studies, such as that of the spreading of the Fraser River plume (Stronach, 1977) or of the formation of tidal frontal areas (Parsons et al. 1981), which were hitherto inaccessible to analysis.

Verification of current predictions are made with current measurements. One verification of particular interest concerns that of residual currents predicted by the model near the southern end of Haro Strait (Fig. 4). Nonlinearity in advection or friction can induce secondary flows, which do not average out over a cycle of a basically periodic motion; headlands (Pingree et al. 1978) and bathymetric irregularities (Loder 1980) commonly lead to the formation of residual flow patterns. Comparison of modeled currents with observed surface drifter motion in Haro Strait confirms the presence of a residual eddy. Residual current eddies of this type at that

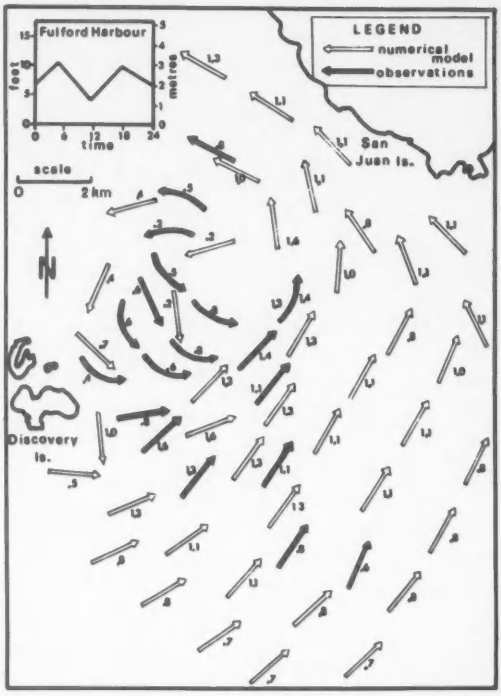


FIG. 4. Comparisons between observed and calculated residual currents over a tidal day in Haro Strait (cf. Fig. 1 for location). Sea level changes at Fulford Harbour during the measurement period are shown in inset. (Courtesy of P. B. Crean)

location as well as in other parts of the Strait of Georgia, such as just north of Boundary Passage, will vary in strength through the fortnightly cycle of neap and spring tides. As discussed by Zimmerman (1980), pulsating tidal eddies provide a mechanism for direct input of tidal energy into slower vortex motions. As we shall see below, the source of the considerable amount of low frequency (5- to 100-d periods) currents in the Strait of Georgia is still unidentified, and it might well be that part of it may be attributed to the tidal rectification phenomenon.

The availability as well the prospect of further refinement and extension of numerical tidal models have opened the door to a new level of analysis of oceanographic phenomena in the Strait of Georgia, whereby the coupling between the highly energetic high-frequency tidal motions with more subtle, longer term oceanographic phenomena can now be studied with some degree of confidence. There remain, however, a significant number of physical problems to resolve as well as improvements to be made to the description of the tides. Details of tidal dissipation, now represented in models in terms of a bottom friction parameter, may have to be elucidated in more detail, particularly with respect to their interactions with the stratification in producing internal waves and

FIG. 5. The Fraser River plume, as seen by the LANDSAT satellite. Muddy water is disgorged, from north to south, out of the North, Middle, and South Arms of the Fraser and out of Canoe Pass (south of the South Arm). The South Arm contributes about 80% of the runoff.

homogenizing the water column. Very high resolution modeling of the tide in regions of abrupt bathymetric change and strong currents as well as calculations of residual currents rely on proper modeling of dissipation and diffusion processes. Residual flows should be calculated for the real tide for periods of a few fortnightly cycles and examined as to their dependence on grid size. Discussion shall return repeatedly to the coupling mechanisms between the tide and other circulation systems.

Estuarine Conditions

Freshwater runoff is the second major factor influencing the

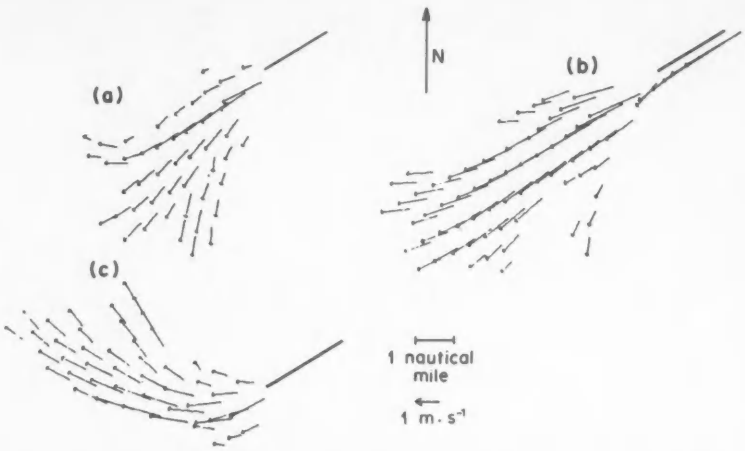


FIG. 6. Surface currents measured with drifting buoys at the mouth of the South Arm of the Fraser River at different stages of the tide. The Steveston Jetty is shown as a solid line in the upper right corner of each panel. (a) At the beginning of a large ebb; (b) at the end of a large ebb; (c) at the beginning of a large flood (1 nautical mile = 1.852 km). Rates of divergence and deceleration of the plume were made from these data by Cordes et al. (1980).

waters of the Strait of Georgia. Runoff, mostly from the Fraser River, determines the internal structure of the water in the Strait: the vertical and horizontal distributions of salinity, and hence of density, and their variations throughout the year. An example of the seasonal variation of runoff in the Fraser is shown in Fig. 9. The Fraser River outflow creates estuarine conditions that range in their downstream extension from the river mouth through all types of the Hansen–Rattray classification (Hansen and Rattray 1966): a tidally pulsed salt wedge in the lower reach of the river itself is followed by the highly stratified "plume" that spreads over the southern and central part of the Strait. Intensive tidal mixing in the passages between the Gulf and San Juan Islands and in the northern accesses to the Strait creates well-mixed conditions in those reaches. Finally, in Juan de Fuca Strait and Johnstone Strait two-layer flow in a more weakly stratified system is restored.

THE SALT WEDGE

Although peripheral to the Strait of Georgia, the saltwater wedge in the Fraser River plays an important role in determining the characteristics of the plume in the Strait itself. It is in the river itself, at the very source of the estuarine influence, that we already observe a strong coupling between the tides and the runoff. The propagation of sea level variations upriver is strongly affected by the river flow (Ages and Woollard 1976). As shown by LeBlond (1978), tidal propagation in such a shallow channel is more appropriately represented as a diffusive than as a radiative phenomenon: the asymmetry in ebb and flow currents associated with the net downstream river flow is responsible, through its influence on frictional forces rather than on the wave propagation speed, for the relative slowness with which the low-water signal travels upstream compared with high water. The salt wedge itself pulsates in and out of the river in response to sea level changes at the river mouth. Although a qualitative understanding of this process has long been at hand (Tully and Dodimead, 1957), studies of the propagation of the wedge into the river as a forced internal tide are relatively recent (Hodgins 1974; Hodgins et al. 1977). The physics pertaining to the nature of the toe of the advancing wedge and to the degradation of the vertical density structure when the wedge is flushed out of the river on ebb tide are still poorly understood. More recent measurements, such as those of Ages (1979), deserve further analysis and comparison with work done in similar situations (Partch and Smith 1978). Finally, there is still no connection between salt wedge models and plume models; Stronach's (1977) plume model (discussed below) uses empirical relations between currents and the phase of tidal sea level variations at Steveston (cf. Stronach and Crean 1978 for the basic data) as a boundary condition at the river mouth. While this method might prove satisfactory during freshet conditions (May–July), when the river flow is strong enough to keep the wedge from advancing upstream of Steveston, it cannot hold over the winter months when the salt wedge may penetrate upstream as far as New Westminster. Under such conditions, the pulsating wedge is to the plume the "tail that wags the dog," and the coupling between the baroclinic flows in and out of the river would seem to be of great importance.

THE PLUME

The Fraser River plume is the showpiece of the Strait of Georgia. Strikingly colored by its suspended sediment load it presents to the aerial observer a pattern of spreading river

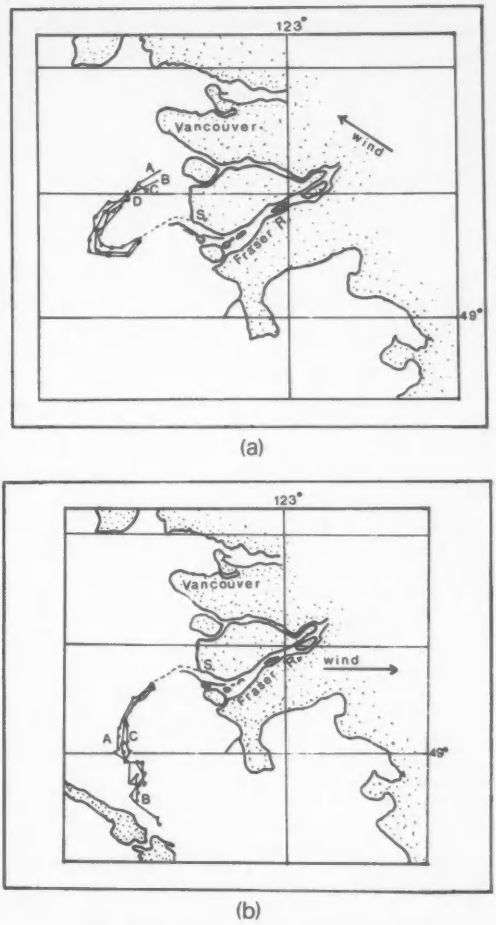


FIG. 7. Paths of surface drogues released at the mouth of the Fraser River at the beginning of ebb flow, showing the influence of wind direction. (a) The four drogues were released 1 h after lower high water and were picked up 12 h later. The wind blew from east–southeast at speeds of 5–10 knots (1 knot = 5 cm·s^{-1}). (b) Three drogues were launched about 2 h after higher high water and picked up (in alphabetical order) successively after 9, 12, and 15 h. The wind blew from the west at about 15 knots. In both cases, the ebbing tide would first tend to take the drogues southward over the first half of the trajectory and then northwards, during flood, over the second half. The effect on the wind accounts for the dissimilarity in the two sets of trajectories.

influence, in milky, brown and green hues. Satellite photographs encompass the whole plume, suggesting dynamics and spreading patterns (Fig. 5). The plume consists of a thin layer (2–10 m thick) of brackish, silt-laden water, which is spread over the Strait by the Fraser River and is particularly pronounced and widespread during summer freshet conditions. There is a sharp density contrast between the plume waters and the saltier waters below; this contrast may tend to decouple the plume from the bulk of the Strait below it in terms of its response to wind forcing, a point to which we shall return in the next section. The relative opacity of plume waters causes them to absorb even more sunlight than would normally contribute to heat the surface layer; this effect strengthens the density contrast associated with the plume. This opacity also decreases the thickness of the euphotic zone, affecting the biological productivity of the Strait. Because the plume determines the water properties of the superficial layer of the Strait of Georgia and conditions their direct response to wind forcing, it has been one of the focal points of local oceanography from the earliest days. Hutchinson and Lucas' (1931) survey was basically one of plume properties. Observations of the plume have explored its dynamics as well as the distribution of its scalar properties.

Observations of plume dynamics, in the form of joint measurements of currents and water properties, have focussed in the near field of the plume, just off the mouth of the Fraser River. In this area the properties of the upper layer are determined by its dynamics, i.e. by the surface sea level slope that pushes it seaward and by the deceleration brought about by friction and entrainment of salt water from below. The drogue-tracking measurements of Cordes (1977) have documented the initial spreading of the plume and have shown how it is swept north and south by rising and ebbing tides (Fig. 6). Combining these results with scalar property measurements taken by de Lange Boom (1976) along the axis of the plume, Cordes et al. (1980) obtained estimates of entrainment rates near the mouth of the river. Further measurements by Stronach and Crean (1978) have been incorporated in the formulation of the upper layer model described below. Overall, the dynamics of the more energetic, younger part of the plume, and of its possible interaction with the salt wedge or with the tidal flow over the banks that surround the Fraser River mouth, are poorly documented. Much remains to be done in describing and understanding the details of the flow patterns near the mouth of the river, especially during the periods surrounding the turns of the tide.

Downstream from the river mouth, drogue tracking of the plume has shown it to be strongly modulated by tidal currents and influenced by wind conditions. Surface current followers released at the mouth of the Fraser at similar stages of the tide follow quite different paths under different wind conditions, as seen in Fig. 7, curving back onto the eastern shore under the influence of winds from the southeast but heading directly across the Strait under the effect of winds from the west. A common pattern, also revealed by a study of the evolution of water color patterns (Tabata 1972), shows a large-scale clockwise wheeling of the surface waters northwards (Fig. 8). J. A. Stronach (Beak Consultants Ltd., Vancouver, personal communication) has conducted drogue tracking experiments that indicate a similar motion. In a different mode, under predominant northwesterly winds, the plume heads south from the river mouth towards Boundary Passage. This is the pattern often seen in satellite photos, available during the good visibility conditions corresponding to winds from that quadrant. One must still be careful not to generalize about the surface circulation in the Strait from the few drogue tracks and

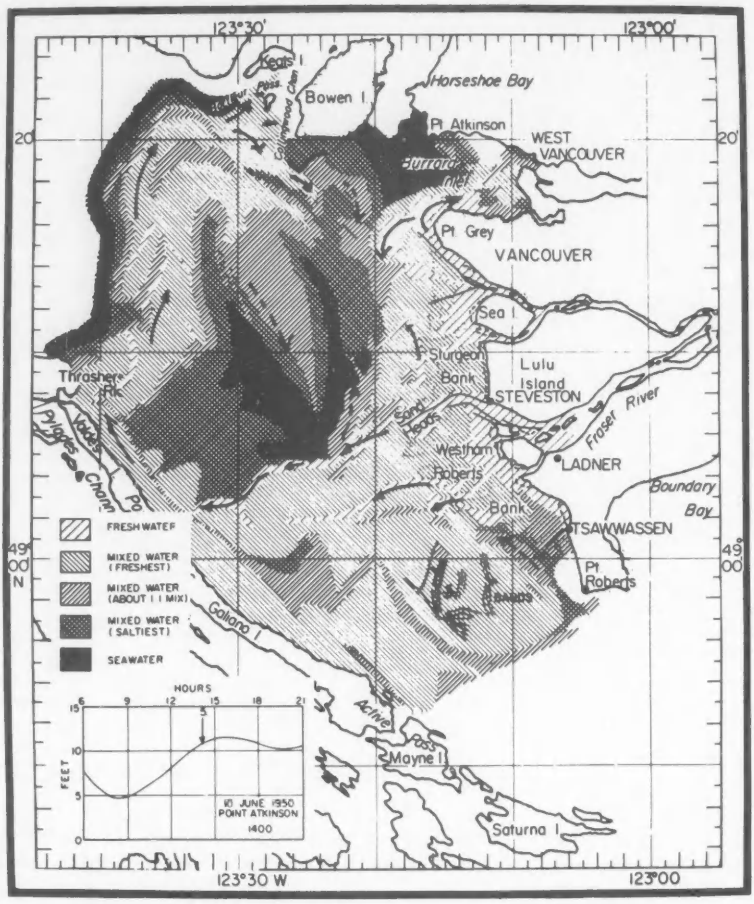


FIG. 8. Surface water salinity and circulation in the Strait of Georgia inferred from observed silt distribution. The arrows indicate inferred flow direction. Note the apparent clockwise flow north of the river. The bands off Point Roberts are internal wave trains. The inset shows the stage of the tide. (From Tabata 1972)

satellite pictures observed. Only a few situations have been examined and we should now know enough about oceanic variability not to create rules and patterns from too little evidence.

A recent survey of the surface salinity of the Strait of Georgia along the British Columbia Ferry routes that join Horseshoe Bay to Nanaimo and, in the south, Tsawwassen (through Active Pass) to Swartz Bay, has provided time series of eight daily transects, which document the evolution of the salinity of the Strait along two lines (Fig. 1) for 2 full yr (Royer and Emery 1980, 1982). This kind of information provides a statistical basis for many properties of the plume, which have so far been gathered on an "event" basis from a few special experiments, occasional observational programs, or good-weather satellite images. An example of the data is seen in Fig. 9, which shows the variation of average salinity along the two transects over the year 1980 in comparison with the strength of the Fraser River runoff. Freshet is reflected by a notable decrease in near-surface salinity at both sections, accompanied by a great degree of variability that is not obviously correlated with that of the runoff itself. Of particular interest in Fig. 9 is the sharp year-end runoff peak, whose immediate effects can be traced in both sampled sections. This event provides a concrete, rather well-documented example of the response of the upper layer to a freshwater impulse.

The motion of the plume, i.e. of the upper layer waters of the Strait of Georgia, takes place under the combined

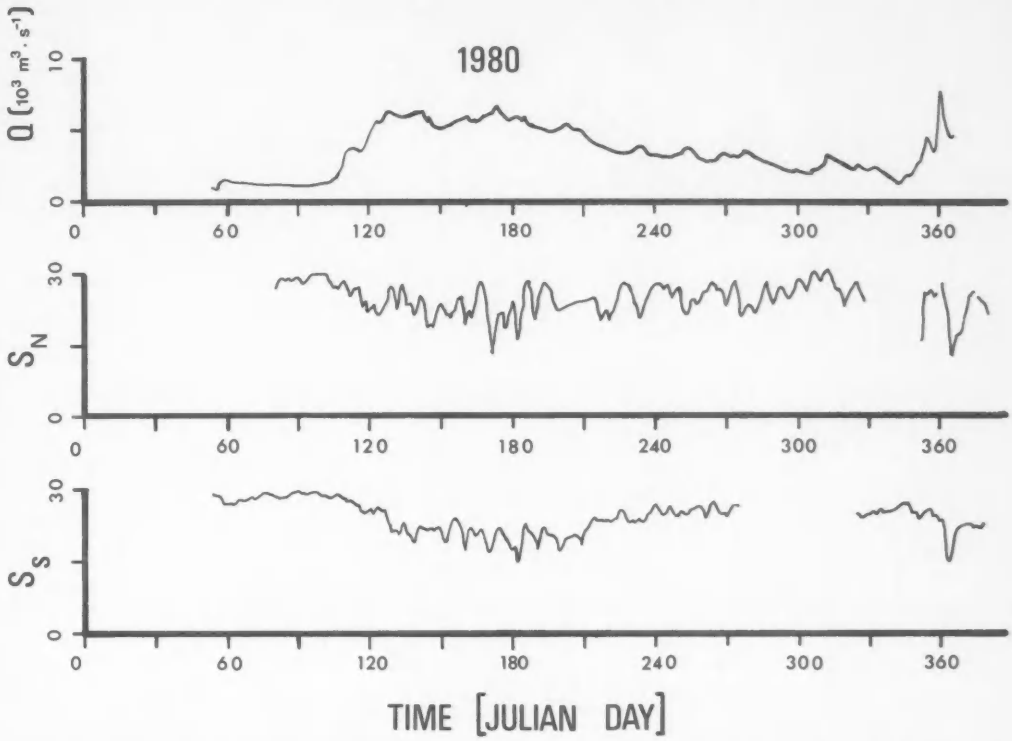


FIG. 9. Average salinity for the year 1980 along the ferry crossing routes shown in Fig. 1 compared with the measured discharge (Q) of the Fraser River (at Hope: 150 km upstream from the mouth). S_N and S_S refer to northern and southern sections, respectively. Note the high variability in salinity during strong runoff conditions at both sections. The high runoff peak of day 362 has a direct repercussion on salinity at both sections, but at the northern before the southern; this is a wind effect discussed in the text. (From Royer and Emery 1982)

influence of tidal pressure gradients, river outflow, and wind stress; friction and entrainment depend on the local Richardson number, determined by the local vertical velocity shear and density gradient. This complex system is not amenable to simulation by analytical methods. Given the recent availability of a barotropic tidal model it was a logical next step to formulate an upper layer numerical model (Stronach 1977, 1981) to pursue studies of the sensitivity of the plume dynamics to different physical parameterizations and to explore its configuration under different discharge, tidal, and meteorological regimes. An example of the type of results provided by Stronach's model is shown in Fig. 10. The upper layer model provides a unified framework around which can be organized more sophisticated investigations of plume dynamics. In order to make the model a practical research tool with which to unravel the evolution of patterns such as those of Fig. 5 and 8, or to explain the salinity time series shown in Fig. 9, much development still seems to be required. Fronts, for example, will have to be dealt with satisfactorily in the numerical simulation; these fronts, usually visible as sharp water color contrasts, are one of the most prominent and most consistently identifiable features of the surface of the Strait, and tracing their motion would seem a reasonable requirement of the numerical model. Meteorological forcing, not presently included, will also have to be included.

THE RETURN FLOW

In a deep estuary, such as the central Strait of Georgia, a surface outflow of brackish water is normally balanced by a deep return flow. Whereas the surface flow is moderately well documented, as discussed above, the return current is very poorly known. Direct evidence of flow at depth into the Strait of Georgia all the way in from the Pacific Ocean was first provided by the recovery of seabed drifters released on the continental shelf (Gross et al. 1969). Indirect evidence of penetration of oceanic waters has been available from the earlier surveys, which revealed the presence of salty water at depth. Current measurements in Juan de Fuca (Fissel and Huggett 1976) and Johnstone straits (Thomson 1976, 1977) have confirmed the presence of a deep residual flow at depth towards the Strait of Georgia. Observations at the southern

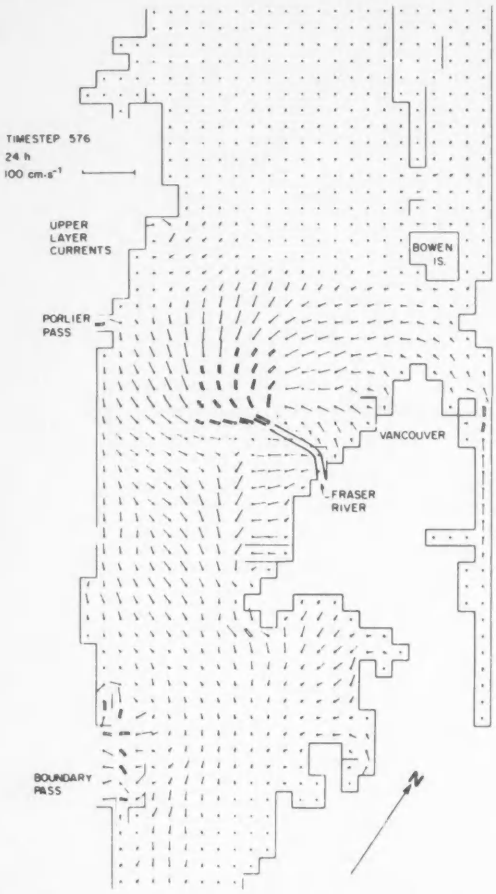


FIG. 10. Typical current map from the upper layer simulation model of Stronach (1981). As indicated, this situation results after 24 h (576 time steps of 150 s each). Tidal current data is updated every 15 min; the situation shown corresponds to flood tide. The grid size is 2 km.

end of the Strait of Georgia by Schumacher et al. (1978) have given indications of inflow through Haro Strait. Within the body of the Strait itself, one would expect that the shape of the basin might affect the spatial distribution of return flow, especially at the deeper levels, and that the circulation picture might be more complex than in the nearly rectilinear approach channels (Juan de Fuca and Johnstone straits). Some recent data of Yao et al. (1982) do indicate a mean flow towards the Fraser River at depth at a location in the center of the Strait (see below, Fig. 21, 23). There are very few current measurements of sufficient duration for statistical reliability in the Strait, and it is not now possible to draw mean streamline maps of the deep estuarine return flow.

The specification of the return flow part of the estuarine circulation is intimately related to the processes of deepwater renewal as well as to the interpretation of the low-frequency variability of deep flows observed in the Strait, matters which I shall discuss in more detail below. Seasonal variability in runoff (Fig. 9) induces, in an as yet quantitatively undocumented way, changes in the strength of the estuarine circulation. There is a lag in the response of the system, as suggested by the net rise in sea level observed in the Strait during the summer (Waldichuk 1964). The complex coupling between the variations in freshwater runoff and the combined effects of tidal and meteorological forcing, mediated by the geometry of the Strait and possible Pacific Ocean influences, is a subtle but extremely important interaction that determines interannual fluctuations in the properties of the waters of the Strait and exchanges with the ocean. This interaction process is very poorly understood.

Atmospheric Inputs

On a global scale, heat and momentum exchanges at the ocean–atmosphere interface are the prime causes of oceanic flows, giving rise to the wind-driven as well as to thermohaline circulation. The Strait of Georgia differs markedly from typical oceanic regions in that the wind and surface heat exchanges are less important, respectively, than the tides and freshwater runoff in producing currents and in affecting the vertical stratification of the water column.

During most of the year, and over most of the Strait, the salinity structure dominates the density stratification because of the strong freshwater runoff. It is only in exceptional circumstances that the temperature of the water plays a dynamic role: whenever the density stratification is weakened, by wind or tidal mixing, small temperature differences may determine whether convection takes place as well as the depth to which it penetrates. These conditions normally occur near the well-mixed extremities of the Strait and play a crucial role in deep and intermediate water formation.

Low-level winds are orographically steered along the major southeast–northwest axis of the Strait of Georgia. Their effect on the usually strongly stratified upper layer is to push it as a slab in the direction of the wind, following the ideas of Pollard and Millard (1970). A direct confirmation of this type of response has been obtained in local waters (Howe Sound) by Buckley and Pond (1976). The response of the Fraser River plume to wind forcing has already been illustrated in Fig. 7. The analysis of salinity variations along ferry routes by Royer and Emery (1982) also confirms a relation between plume position and wind direction. The intriguing response to the late December 1980 (day 360 in Fig. 9) runoff peak, whereby the salinity decreases at the northern section before it does at the southern one, in spite of the latter's greater proximity to the river, is also explainable in terms of wind effects. The fresher water is first pushed northwestward, towards the northern ferry crossing, by a southwest wind; it is only later on day 364, when the wind changes direction, that the salinity decreases at the southern section.

By generating waves, winds are also indirectly responsible for the longshore currents induced by the former when they break along the shore. The ensuing sediment transport causes

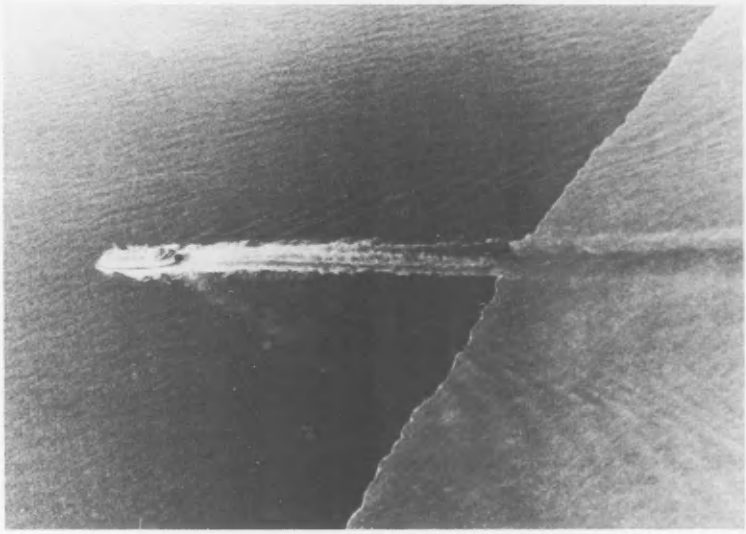


FIG. 11. A sharp riverine (or estuarine) front separating muddy brackish Fraser River plume water on the right from cleaner, saltier oceanic water on the left. The ship is one of the ferries plying the southern route shown in Fig. 1.

erosion as well as deposition, gnawing at the feet of cliffs and leaving spits in their lee. This process gradually modifies the bathymetry, affecting in turn the nature of waves and currents in a long-term feedback loop.

Obvious wind effects are limited to the upper layers of the Strait. Attempts at relating long-term (periods >5 d) wind fluctuations to similar variations of flow measured at depth (Chang 1976; Helbig 1978) have generally revealed low correlations between winds and deep currents. Atmospheric pressure fluctuations do account for over 60% of daily and seasonal sea level fluctuations in the Strait (Waldichuk 1964). However, long-term (>5 d) pressure variations have not been found (Chang 1976) to be correlated with deep currents. There is thus far no evidence of a direct dynamic relationship between atmospheric inputs and the slow, deep circulation of the Strait.

Fronts

Fronts are regions of strong horizontal gradients of scalar properties, usually accompanied by appreciable current shears. Frontal regions separate different water masses at their point of convergence; they are found on a wide range of scales from the tens of kilometres of oceanic structures such as the Subarctic Convergence to the few metres of small riverine (or estuarine) fronts near river mouths. A recent review of frontal studies by Bowman and Esaias (1978) is an excellent introduction to the subject. In the Strait of Georgia, one encounters three types of fronts: riverine and tidal mixing fronts, which result from direct interaction between tidal and estuarine conditions, and headland fronts, which involve in addition a geometrical convergence caused by the form of the coastline.

Riverine Fronts

The main runoff input into the Strait of Georgia flows through the Fraser River; this outflow is pulsated as the tide ebbs and flows into the river. On the flood tide, water from the Strait is pushed upstream; the upper brackish layer left in the Strait continues to mix with the salt water below it through wind mixing and internal wave dissipation. On the ebb tide, new freshwater floods the upper layer of the Strait. A sharp horizontal transition is formed between this very fresh water and the already brackish water outside the river mouth; a riverine (also estuarine) front appears (Fig. 11). Such fronts are strong convergence zones and normally collect flotsam and debris — mariners call them "tide lines." They are difficult to study because of their small overall scale, their rapid translation rate, and their vigorous dynamics. Stronach (1977) presented some observations of riverine fronts within the Fraser River plume. Similar fronts also occur at the tidally mixed extremities of the Strait in response to fluctuating tidal currents. Nof (1979) discussed a front in Haro Strait and presented a theory of front generation by mixing and intrusion, which may account for the rapid sharpening of fronts observed in coastal regions, where water masses of widely different salinities are often juxtaposed. Nof's mechanism has yet to be verified in the field; the Strait of Georgia, with its abundance of frontal structures, might be just the place to do it. The dynamics of riverine fronts has not yet been included in the upper layer modeling process. Their visibility and the ease with which they can be followed by remote sensing methods (e.g., see Fig. 8) makes them ideal two-dimensional tracers of the water masses that they bound; it is thus

FIG. 12. A headland front off the southeastern tip of Point Roberts.

imperative that they should eventually be incorporated within plume models. Riverine fronts are akin to "plate boundaries" between successive tidally pulsed discharges of river water; their evolution documents the spreading of the upper layer.

HEADLAND FRONTS

Headland fronts result from a geometrically induced convergence in the vicinity of headlands or other coastal or bathymetric structures. Tidal currents are often involved. A striking example near Portland Bill (on the southwest coast of England) has been discussed by Pingree et al. (1978). An example of a headland front off the southeast end of Point Roberts is shown in Fig. 12. Such features are very local in character but may have some small-scale importance in concentrating sediments and pollutants. Their location is often associated with spits or banks, which may in turn owe their existence to wave-generated longshore sediment transport.

TIDAL MIXING FRONTS

A tidal mixing front is a region of transition between a vertically homogeneous water mass, mixed by strong tidal currents in shallow water, and vertically stratified waters found where the currents are weaker and the depth is greater. This kind of front is on a scale of a few kilometres and is defined by the mean properties of an area, averaged over a few tidal cycles. The tidal mixing frontal region may include

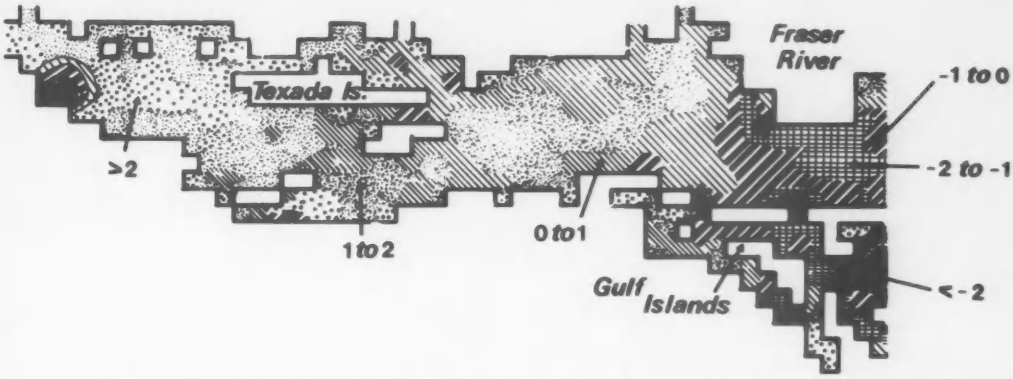


FIG. 13. Map of the modified stratification index $E = \log(H/U^3)$ for the Strait of Georgia, where H is the water depth and U is a typical tidal current speed. With a drag coefficient $C_D = 2 \times 10^{-3}$ the transition value $\log M = 1.5$ between mixed and stratified regions corresponds to $E = -1.0$. Lightly shaded areas in the central Strait correspond to strong stratification ($E > 0$); dark shades, near the northern and southern passages, are well mixed ($E < 0$). (From Parsons et al. 1981)

within it a finer structure, in space and time, consisting of sharp riverine fronts that migrate across the broader frontal zone, alternately sharpening and dissolving with the changing phases of the tide. Fernhead (1975) introduced the stratification parameter $M = H/C_D U^3$ (H = depth, C_D = drag coefficient, and U = mean tidal velocity), which expresses the ratio of stratifying effects (buoyancy fluxes due to insolation or runoff) to the mixing power of the tide. Parameter M is large in deep water (large H), where tidal currents are too weak to mix the water column, and small in shallow areas of strong tidal streams, where the stratification disappears because of tidal mixing. Tidal fronts occur at a certain transitional value of M.

Pingree (1978) and Simpson et al. (1977) found the transition at about $\log M = 1.5$ around the British Isles. Bowman and Esaias (1981) obtained similar results in Long Island Sound, but Garrett et al. (1978) found a higher value ($\log M = 1.9$) in the Bay of Fundy. The exact value of M at the transition between well-mixed and stratified environments depends on the magnitude of the surface buoyancy flux, due to insolation or runoff, which tends to stratify the water column. One would thus expect regional differences. It would be surprising, in particular, to find that the results obtained in a mainly thermally stratified area, such as around the British Isles, apply unmodified to a coastal sea, such as the Strait of Georgia, where runoff is the main factor affecting the density structure.

The availability of a numerical model of tidal currents makes it possible to calculate the mixing parameter with a fine resolution over a wide area. Parsons et al. (1981) used Crean's (1978) tidal model to evaluate M in the Strait of Georgia; their results (Fig. 13) show transitional regions at the northern and southern ends of the Strait, in the vicinity of the turbulent passages that connect it to the ocean. These tidal mixing fronts have been found to be zones of enhanced biological productivity; there are indications that biological effects may extend up to the level of fish abundance in some frontal areas (Fournier 1978).

The interaction between meteorological, estuarine, and tidal systems, which determines the existence and the properties of tidal mixing fronts, has far-reaching consequences on the marine environment. Its biological consequences alone would make it a worthy subject of further study. As we shall see presently, this interaction also plays a crucial role in determining the conditions that lead to deepwater renewal in the Strait of Georgia.

Deepwater Renewal

What determines the properties of the deep water of the Strait of Georgia? This kind of question has always been of fundamental interest for physical oceanography. Noticeable seasonal changes in temperature, salinity, and dissolved oxygen are observed at depths well below the deepest level of direct atmospheric influence. Seasonal and interannual variations in temperature, salinity, and dissolved oxygen at depth at a central location in the Strait of Georgia over a 7-yr interval are shown in Fig. 14 (from Pickard 1975). Temperature and salinity vary nearly in phase over a year, reaching their maximum values during the fall. The variance in both decreases with depth, but there is still a considerable degree of variability at 300 m, with a range of 0.5‰ in salinity and 1.0°C in temperature. Deep oxygen values reach their maximum in late spring somewhat before the minimum values of temperature and salinity occur.

Waldichuk (1957) proposed a model whereby deep water is formed at the tidal mixing regions of the northern and southern ends of the Strait when meteorological, estuarine, and possibly offshore dynamic influences conspire to create a water mass of a density sufficient to make it sink towards the bottom of the Strait. In late winter, cold deep water is formed in the south; a cold intermediate water layer may also form in the north. Sinking of these water masses accounts for the minima of temperature and salinity seen in Fig. 14. In late summer and fall, a deep saline intrusion penetrates the Strait from the south to form intermediate and deep water; this

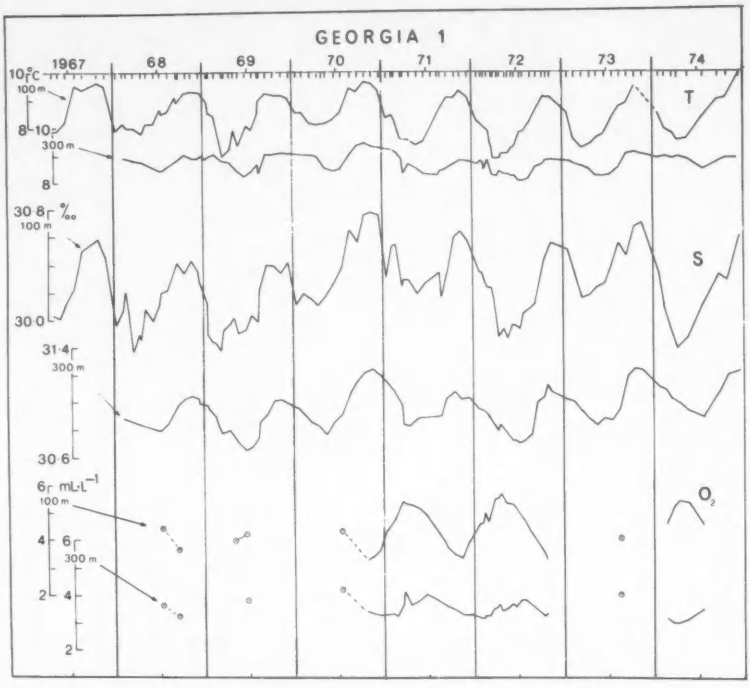


FIG. 14. Long-term variation of oceanographic properties (temperature, T, salinity, S, and dissolved oxygen, O_2) at depths of 100 and 300 m in the central Strait of Georgia. Station location is shown by the triangle in Fig. 1. (From Pickard 1975)

intrusion is responsible for the salinity and temperature maxima of Fig. 14. The deepwater renewal processes hypothesized by Waldichuk (1957) are shown schematically in Fig. 15. It is interesting to note that the winter and summer mechanisms for introducing dense water at depth are really quite different. In the winter, very cold but relatively fresh water of near-surface origin (as evidenced by its high oxygen content) is formed by some vigorous mixing process in the tidal passages. In the summer, on the other hand, at a time when the surface waters are at their freshest, it is an inflow of salty water at depth from outside the Strait that penetrates to great depths. This latter process clearly involves some external influence: an intrusion of Juan de Fuca waters into Haro Strait. Does the increase in runoff during summer freshet drive an enhanced return flow, which brings in deeper, more saline water? Or do the waters of Juan de Fuca Strait shift in adaptation to summer meteorological or oceanic conditions (upwelling along the coast)? Our understanding of the mechanisms responsible for the deepwater renewal, as inferred from observed property changes, has progressed only little since Waldichuk's (1957) classical description.

The most extensive synoptic observations of water properties in the Strait of Georgia, providing broad spatial as well as temporal coverage, have been those carried out by Crean and Ages (1971) in 12 monthly cruises through 1968. A study of these data by Samuels (1979) has confirmed in part Waldichuk's ideas on deepwater renewal. Significant differences and additional details were also found. Two separate large-scale intrusions were noted in the 1968 data. In winter, between February and May, cold, well-oxygenated water with a slightly lower salinity displaced the warm water left from the previous summer. In summer and autumn, warm, saline water with a relatively low oxygen content intruded to the bottom. This intrusion began between May and August 1968 and continued through November. Both intrusions entered the Strait through its southern extremity and progressed northwards. No cold intermediate water was formed in the northern region during 1968; in addition, the warm summer intrusion penetrated to the very deepest parts of the Strait rather than forming an intermediate water, as suggested by Waldichuk.

The progress of the summer intrusion into the deep Strait can be followed at the 175- to 200-m level in Fig. 16a–c; the warm water mass is observed to travel more rapidly northward on the east side of the Strait. The warmer water does not reach the bottom: colder water is still present at greater depths (Fig. 16d). The increase in salinity associated with the intrusion can, however, be traced in the deepest layer so that the densest intruding water does indeed reach the bottom of the Strait.

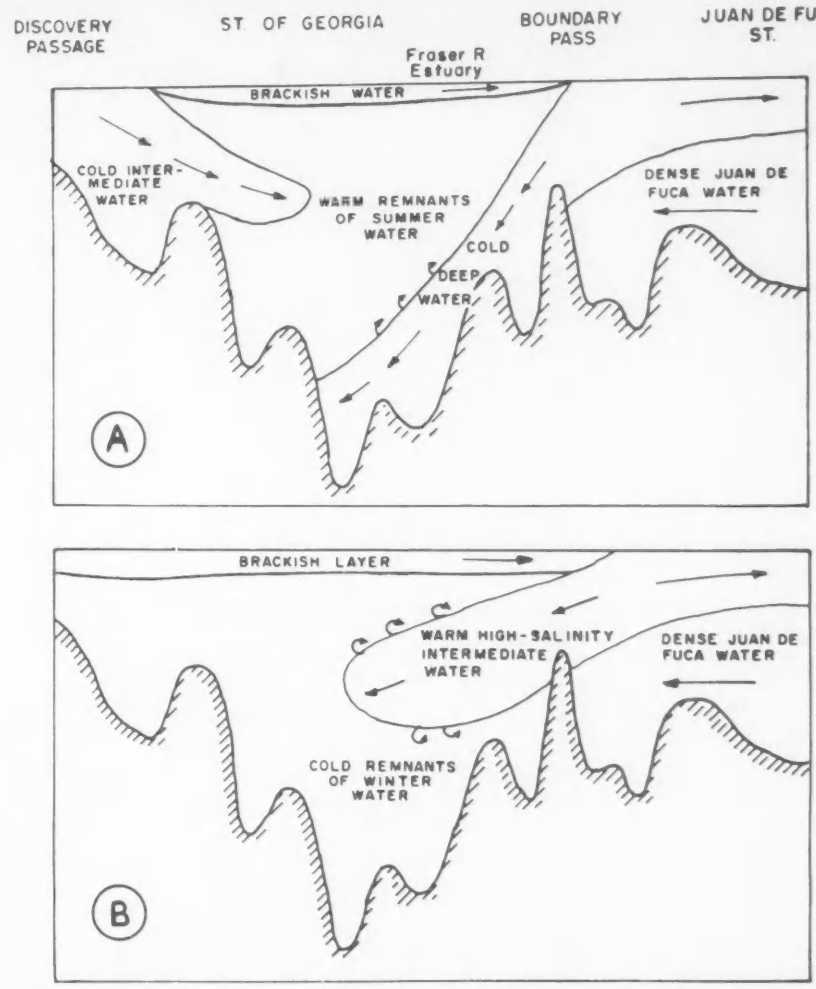


FIG. 15. Deepwater formation mechanisms in the Strait of Georgia, according to Waldichuk (1957). (A) late winter; (B) late summer.

Samuels' (1979) interpretation of the evolution of deepwater properties indicates a nearly continuous replacement going on, with occasional intensification, rather than strong intermittent overturns. Deepwater renewal in the Strait of Georgia should be viewed as an ongoing process, part of the return flow of the estuarine circulation, which occasionally penetrates to greater than usual depths because of varying water conditions at the well-mixed extremities of the Strait. Some short-term current measurements in the southern Strait by Schumacher et al. (1978) indicate deepwater exchange mainly through Haro Strait, the westernmost and deepest of the passages linking the Strait of Georgia to Juan de Fuca Strait.

The beginnings of a more quantitative study of deepwater renewal have been made by P. B. Crean (Institute of Ocean Sciences, Sidney, B.C.), using a laterally integrated two-dimensional numerical model, which includes stratification and tidal mixing. Shown in Fig. 17a and b, respectively, are the initial and final salinity structures in a model in which the density stratification is modified by mixing, creating in Boundary Passage a dense water mass that sinks to the bottom of the Strait. The progress of the 32‰ isosaline into the Strait is clearly evident. The secondary circulation in the vertical plane is shown in Fig. 17c. While these numerical

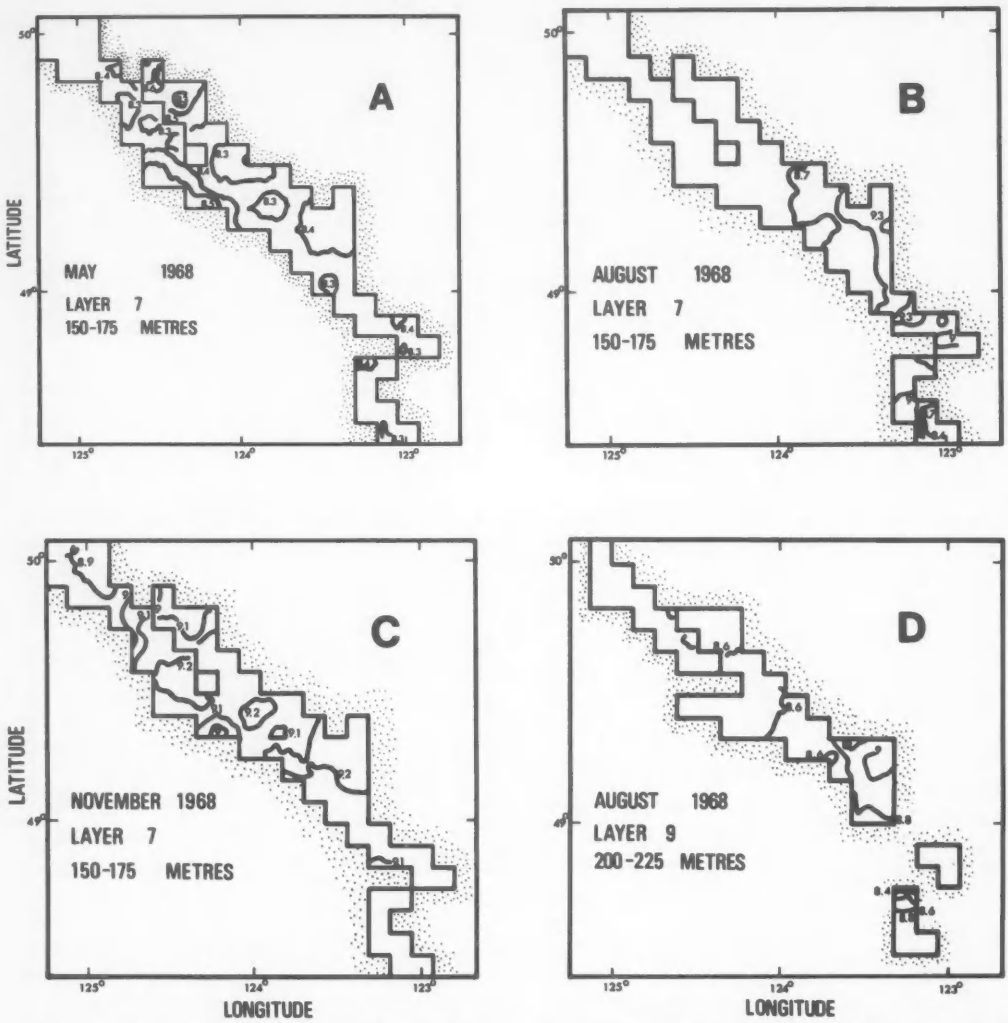
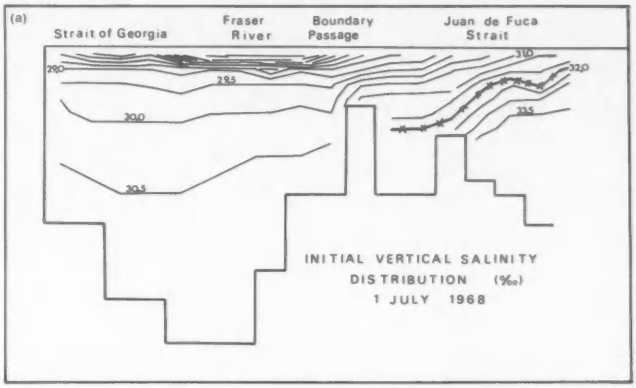
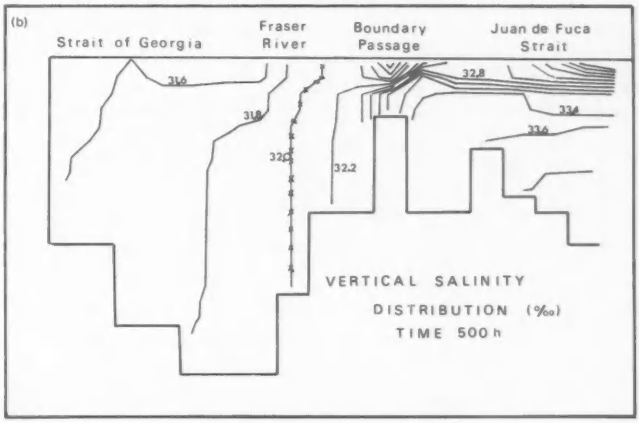


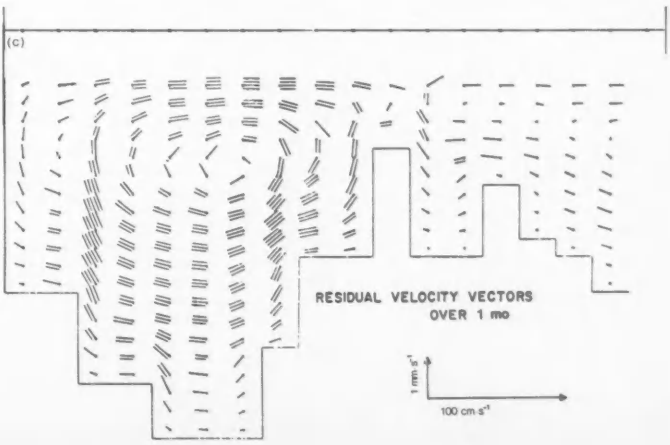
FIG. 16. Temperature distributions at depth in the Strait of Georgia in 1968, contoured from the data of Crean and Ages (1971) and digitized by Samuels (1979). (A–C) Temperature contours (degrees Celsius) for a 25-m-thick layer between the depths of 150 and 175 m in May, August, and November, showing the penetration of a warm water mass; (D) temperature in a lower layer in August; the warmer water did not reach down to that level.

experiments are still preliminary and seem to produce excessively vigorous vertical motion, they do represent a contribution towards a better understanding of the deepwater renewal process.

FIG. 17. The evolution of the salinity structure in a two-dimensional, laterally integrated numerical model that incorporates mixing at the shallow sill in Boundary Passage. (a) The initial salinity distribution; the 32.0‰ isohaline is enhanced for reference. (b) Salinity distribution 500 h later; the 32.0‰ isohaline has now penetrated the Strait of Georgia. (c) The residual circulation pattern accompanying the water renewal process. (Courtesy of P. B. Crean)


(a)
Strait of Georgia
Fraser River
Boundary Passage
Juan de Fuca Strait
29.0
29.5
30.0
30.5
31.0
32.0
32.5
INITIAL VERTICAL SALINITY DISTRIBUTION (‰)
1 JULY 1968


(b)
Strait of Georgia
Fraser River
Boundary Passage
Juan de Fuca Strait
31.6
31.8
32.0
32.2
32.8
33.4
33.6
VERTICAL SALINITY DISTRIBUTION (‰)
TIME 500 h


(c)
RESIDUAL VELOCITY VECTORS OVER 1 mo
1 cm s⁻¹
100 cm s⁻¹

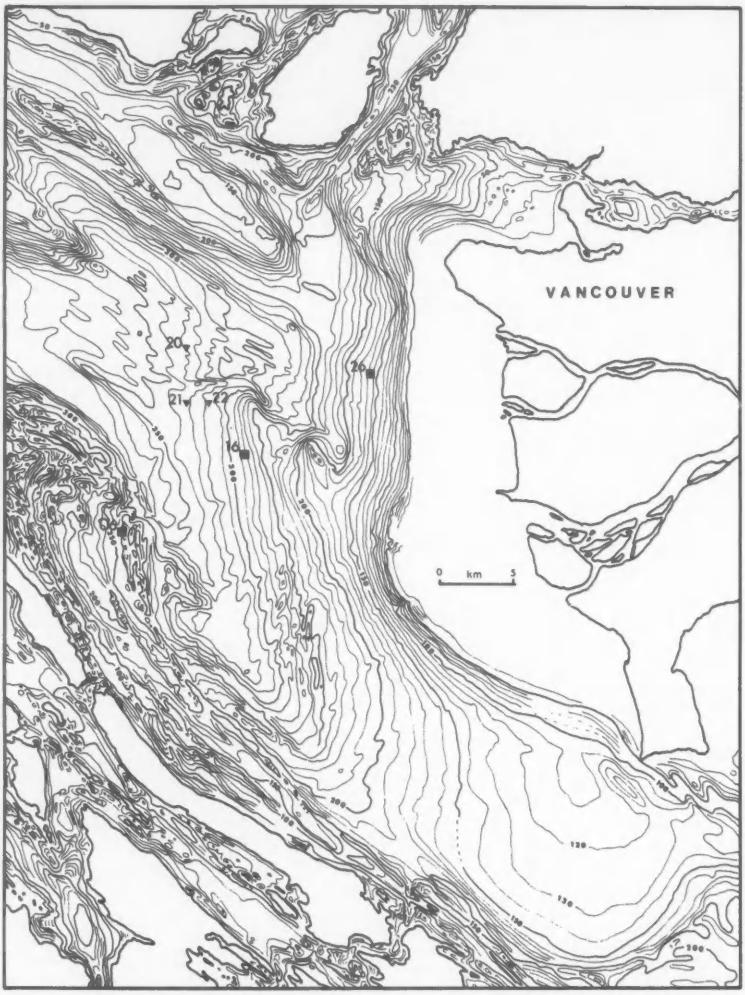


FIG. 18. Detailed bathymetry of the southcentral Strait of Georgia, showing the position of moorings H-06, H-16, and H-26 analyzed by Chang (1976) and of moorings 20, 21, and 22 described by Yao et al. (1982).

Deep Residual Flows

From the earliest current measurements at depth in the Strait of Georgia (Pickard 1956), it was clear that most of the variance of currents, at all levels, was to be found in the tidal frequency bands. Subsequent measurements, taken over periods of up to about a month, confirmed this finding (Tabata et al. 1970a, b, c, 1971). From all these rather short sampling periods, it was not quite possible to extract a reliable estimate of residual flow over, say, a fortnightly tidal cycle. It was, however, generally expected that the fortnightly averaged residual flow would be a meaningful indicator of the residual circulation in the Strait, and that below the pycnocline, this circulation would be related to the estuarine return flow and to deepwater renewal processes.

It was not until the measurements of Tabata and Stickland (1972a, 1972b, 1972c) that long enough time series of current data became available to examine the behavior of residual flows. The measurements came from three moorings, about 10 km apart, placed across the Strait of Georgia as shown in Fig. 18. Each mooring included a current meter at a depth of 50 m; meters were also placed at a depth of 200 m

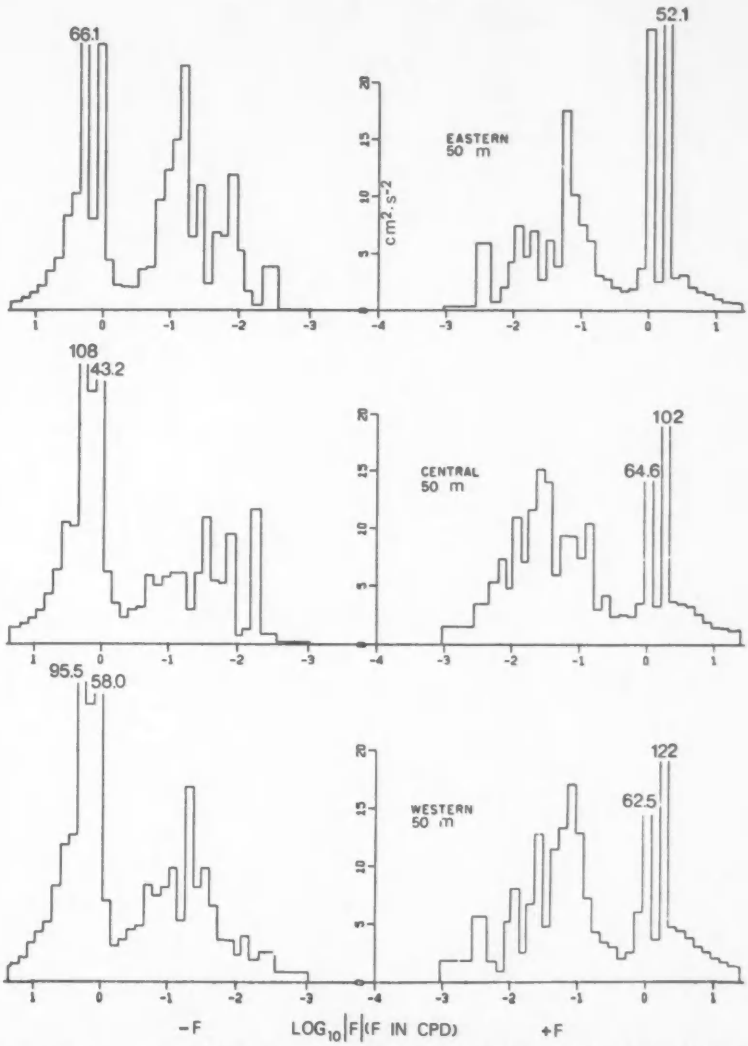


FIG. 19. Rotary spectra (of clockwise motions on the left, anticlockwise on the right) of horizontal kinetic energy at moorings H-06 (western), H-16 (central), and H-26 (eastern), located as shown in Fig. 20. The tidal energy is present at a high level in two narrow bandwidths; an about equal amount of low-frequency energy is spread over a much wider bandwidth and does not exhibit sharp spectral peaks. (From Chang 1976)

at stations H-06 and H-16 and at 140 m at H-26. The data were originally obtained to provide observational verification for Crean's numerical tidal model (Crean 1976). A preliminary analysis of the data quickly revealed that the residual flows were quite variable and that the simple expedient of a fortnightly average could not yield a meaningful residual flow vector, a point that we have already illustrated in Fig. 2. A more thorough analysis of the currents at the three moorings by Chang (1976) and Chang et al. (1976) revealed an even more startling situation. The amount of low-frequency horizontal kinetic energy associated with slowly varying currents over a broad band of periods ranging from 5 to 100 d was found to be comparable with the horizontal kinetic energy of the tides (Fig. 19). In other words, the loosely defined, slowly varying "mean" flow superimposed upon the tide was responsible for as much horizontal motion as the tides

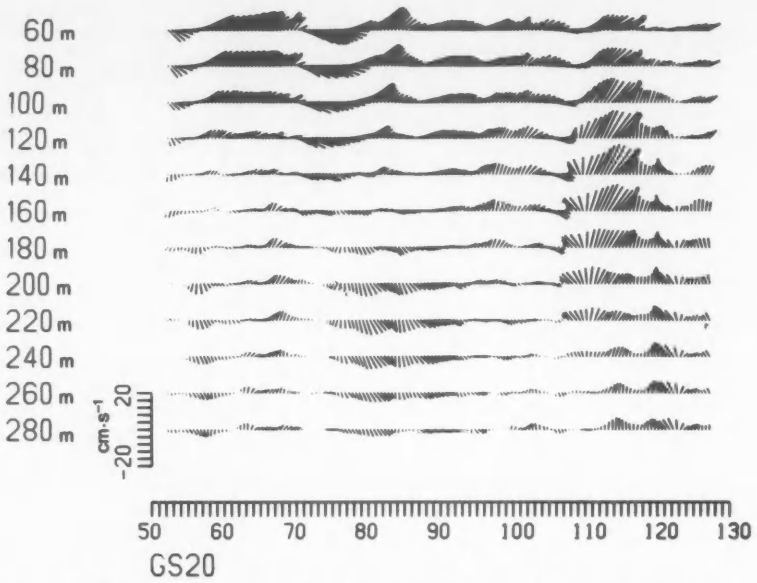


FIG. 20. Daily averaged current vectors at Cyclesonde mooring GS 20 (location shown in Fig. 18) plotted against day of the year, showing slowly fluctuating residual flows and their depth dependence. The mean motion is predominantly towards the east. (From Yao et al. 1982)

themselves. Or again, the residuals were as important as the tidal fluctuations, as is also apparent from a second glance at Fig. 2. The low-frequency fluctuations were not correlated with meteorological conditions or with river flow variations; their intensity decreased approximately linearly with depth from a maximum at the upper instruments (at 50 m). Finally, no significant correlation could be found between the residual flows at the different moorings: the correlation scale was smaller than the station separation! More recent measurements made with Cyclesondes by Yao et al. (1982) at a denser array near the center of the Strait (also shown in Fig. 18) reveal that low-frequency current fluctuations are well correlated for separations of up to 4 km. The high vertical resolution afforded by the Cyclesondes shows some trapping of the motions near the bottom, which counters the general energy decay with depth (Fig. 20), as well as some steering of the bottom flow in the direction of the depth contours. The net trend of the currents observed by Yao et al. (1982), clearly seen in the stick diagrams of Fig. 20, is towards the British Columbia mainland, with strong fluctuations towards the northwest and southeast, along the main axis of the Strait. To sum up, the low-frequency variability observed at depth in the central Strait seems high enough to make any early drift or property transport predictions meaningless. The lack of spatial correlation over separations of more than 10 km indicates that different parts of the Strait behave independently at low frequencies and that there may not exist a consistent large-scale residual circulation pattern; chaos underlies the apparent regularity of tidal flows and the simplicity of estuarine dynamics!

These observations have already provoked several attempts at theoretical explanation. Initial efforts to explain the low-frequency motions in terms of topographically trapped Rossby waves (Helbig and Mysak 1976) failed to account for the small horizontal scales as well as for the observed decay of energy with depth. More sophisticated attempts to extract significant spatial correlations using the line of the three moorings H-06–H-26 as well as other adjacent moorings occupied over shorter time intervals, in terms of plane wave models (Schott and Mysak 1980), have also been unsuccessful. A glance at the detailed bathymetry of the Strait (Fig. 18) does suggest that the bottom configuration is much too complex to expect simple topographically trapped plane wave propagation; in the range of frequencies of interest, wavelengths calculated by Helbig and Mysak (1976) ranged from 25 to 100 km. The broad bandwidth and low correlations of the observed currents are indeed more suggestive of turbulence than of wave motion!

The ideas expressed by Rhines (1977) on geostrophic turbulence as a model for small-scale oceanic eddies might find some application in the Strait of Georgia. It is observed that the low-frequency current fluctuations are uncorrelated with likely low-frequency forcing mechanisms. The fluctuations are thus not a direct response of the basin waters to external stimulus but may result from an internal redistribution of energy from other, probably higher-frequency energy sources such as the tide (or its fortnightly pulsed residual effects). Strong nonlinear interactions between motions of various time and space scales are of the very nature of turbulence; geostrophic turbulence is a special case in which the flow remains

purely horizontal. Some scaling arguments suggest that the low-frequency dynamics of the Strait may be better described in terms of a nonlinear turbulent regime than by linear wave models.

Let us assume that the low-frequency fluctuations are characterized by a correlation scale $L = 5$ km. With a typical velocity value $U = 0.1\ \mathrm{m \cdot s^{-1}}$, the Rossby number of the flow is $Ro = 0.2$, indicating quasigeostrophic dynamics. A bottom slope typical of the area of the current measurements of Yao et al. (1982), where a change of depth of 100 m takes place in 10 km in a water depth of about 300 m, gives an equivalent β (rate of change of Coriolis parameter with position) $= f\nabla H/H \simeq 0.3 \times 10^{-8}\ \mathrm{m^{-1} \cdot s^{-1}}$. The horizontal wavenumber above which nonlinearity exceeds the β effect in the vorticity balance for barotropic motions is (Rhines 1977) $k^* = \sqrt{\beta/U} \simeq 3 \times 10^{-4}\ \mathrm{m^{-1}}$, corresponding to a length scale $L^* = 2\pi/k^* = 30$ km (U is the horizontal current speed). A similar estimate for bottom-trapped baroclinic waves with the critical wavenumber given by $k' \simeq NU$ $(\nabla H/H)$ gives, for $N \simeq 4 \times 10^{-3}\ \mathrm{s^{-1}}$ near the bottom, $k' \simeq 10^{-4}\ \mathrm{m^{-1}}$ and $L' = 2\pi/k' \simeq 62$ km (N is the Brunt–Väisälä frequency). In both cases, these estimates are much longer than the observed correlation scale so that it looks as though the vorticity dynamics of low-frequency motions in the Strait may be significantly nonlinear. One should perhaps seek an explanation of observed residual current variability and spatial structure in terms of geostrophic turbulence ideas rather than through a wave propagation model. These questions remain unsolved and will undoubtedly occupy theoreticians and observers for some years to come. From a practical point of view, the observed properties of the low-frequency variability raise serious problems for long-term modeling of the oceanographic behavior of the Strait; the effects of low-frequency turbulence are vastly more difficult to predict than those of a regular, well-ordered residual flow!

Exchanges With The Ocean

A matter of great interest in the study of coastal basins and semienclosed seas is the rate at which their waters are exchanged with the adjacent ocean. This rate is sometimes expressed in terms of a "flushing time," which is taken as a gross measure of the capacity of the basin to rid itself of pollutants or to reoxygenate itself. In a basin such as the Strait of Georgia, receiving a large volume of freshwater, exchange with the ocean is intimately related to the estuarine circulation set up by the runoff; freshwater continuously flows out to sea in the upper layers, entraining a large volume of salt water with it, while saltier water returns at depth to replace that which has been entrained seaward. There is obviously a close connection between deepwater renewal, as discussed above, and water exchange with the ocean.

A coarse estimate of the freshwater residence time in an estuarine basin may be obtained by dividing the total volume of freshwater present by the net rate of freshwater input (runoff and precipitation minus evaporation). Waldichuk (1957) performed the calculation using 1950 data, assuming that all water in the Strait with a salinity below 33.8‰ was diluted with locally derived freshwater; he obtained an estimate of 1.3 yr for the freshwater residence time. Samuels (1979), using Crean and Ages' (1971) data, found estimates of about 400 d for the total freshwater volume; an estimate of the replacement rate in the upper 50 m, where most of the freshwater is found, gives much shorter times: 80–100 d. From all accounts, it is thus clear that the Strait of Georgia as a whole has a rather rapid water replacement rate for a semienclosed coastal basin. The yearly renewal of deepwater noted above (Fig. 14) confirms the results of flushing time calculations.

Global calculations, however, obscure interesting details. There may be areas or sub-basins where the flushing rate is much slower than the average. Samuels' (1979) analysis indicates that this might have been the case in 1968 for the deeper part of Malaspina Strait, where low dissolved oxygen values were observed. A global estimate also gives no indication of the partition of ocean–basin exchange between the various channels connecting the two. It is reasonable to assume, following Waldichuk (1957), that because of the relatively small cross-section of the northern channels with respect to that of the southern channels (1/15) and of the relative shallowness of the former (maximum 100 m against about 250 m in Haro Strait) most of the exchange with the ocean takes place in the southern passages. Indeed, Waldichuk's (1957) estimates of exchange based on salinity conservation assumed negligible net flow through Johnstone Strait.

To resolve the issue, an ambitious program of current measurement in Johnstone and Juan de Fuca straits was undertaken by the Institute of Ocean Sciences, beginning around 1973, to obtain direct estimates of the exchange rate between the Strait of Georgia and the ocean. Measurements in Johnstone Strait have been reported by Huggett et al. (1976, 1980) and analyzed by Thomson (1976, 1977). Data from Juan de Fuca Strait have been presented and commented on by Fissel (1976), Fissel and Huggett (1976), Huggett et al. (1976), and Godin et al. (1981a). Further current information, collected by United States agencies and including surface drifter and HF current-mapping radar data, have been presented by Cannon (1978), Holbrook et al. (1980a, 1980b), and Frisch et al. (1981). Current measurements in both straits generally confirm the expected two-layer residual circulation: the upper and lower layer volume flow rates, V_0 and V_1, respectively, are nearly equal in absolute value, and the salt and volume budgets are balanced by the relatively small difference between them. The vertical and cross-channel structure of the residual flow in Johnstone Strait is illustrated in Fig. 21. Estimates of V_0 in Juan de Fuca Strait range from 90 to $160 \times 10^3\ \mathrm{m^3 \cdot s^{-1}}$, and in Johnstone Strait from 15 to $50 \times 10^3\ \mathrm{m^3 \cdot s^{-1}}$, so that there is indeed considerably more exchange in the southern access to the Strait of Georgia.

Even with direct measurements of volume inflow and outflow, it is not simple to pin down a reliable estimate of the net exchange rate. First of all, we note that the net exchange is a small difference between two large, nearly equal transports. Godin et al. (1981b) examined the errors involved in choosing a level of no motion in sections such as that shown in Fig. 21b. They concluded that, because of the sparseness of the sampling points, these errors are comparable with the difference estimate sought and that a denser array of current meters would be necessary to provide reliable transport estimates. Godin et al. (1981b) also showed that there was very little agreement between net flows calculated from current

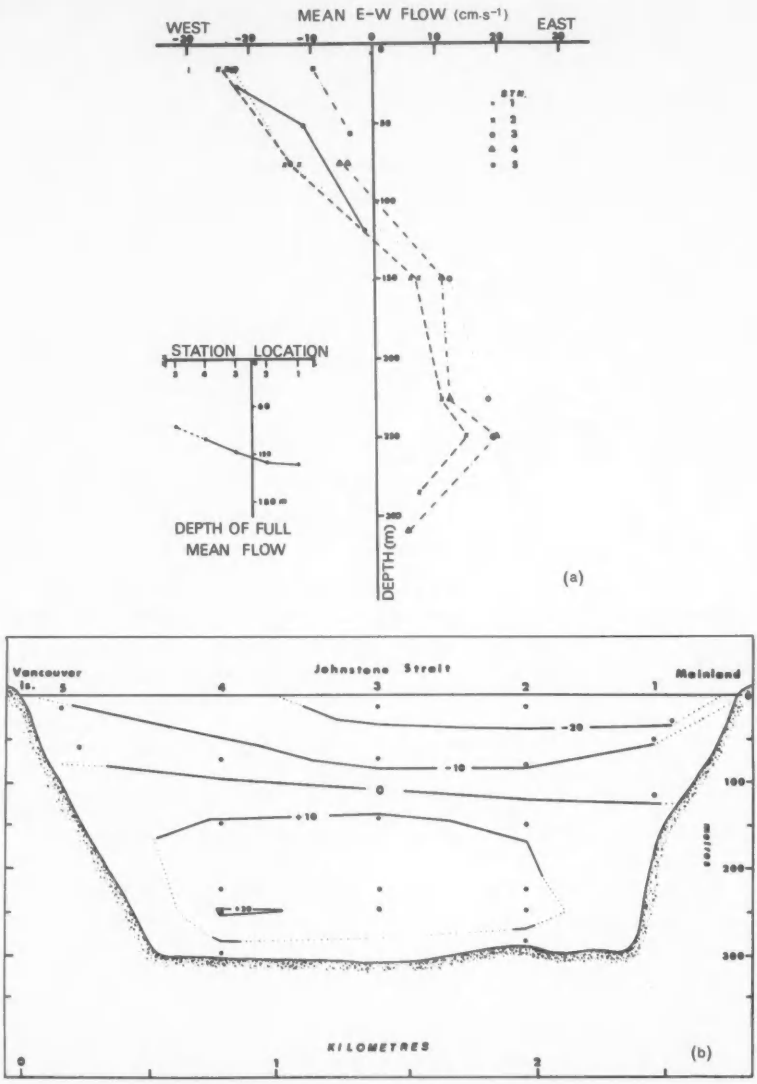


FIG. 21. The two-layer residual flow structure in central Johnstone Strait. (a) Average vertical profiles of along-channel flow; the inset shows the variation of level of zero-mean flow across the channel. (b) Time-average structure, in the cross-channel direction, of along-channel flow. Speeds are centimetres per second, positive inward (eastward), negative seaward (westward). Dotted lines represent uncertain interpolated values. (From Thomson 1977)

meter sections and flows required by continuity as calculated from simultaneous measurements of sea level in the Strait of Georgia. In addition, moored current meters as well as surface drifters have revealed a strong variability of flow pattern in Juan de Fuca Strait, where most of the exchange would seem to take place. The surface flow actually reverses for a few days (Fig. 22) during periods of strong southerly coastal winds (Fig. 23). This kind of sensitivity to oceanic influences introduces further sources of error in the measurement of residual transports.

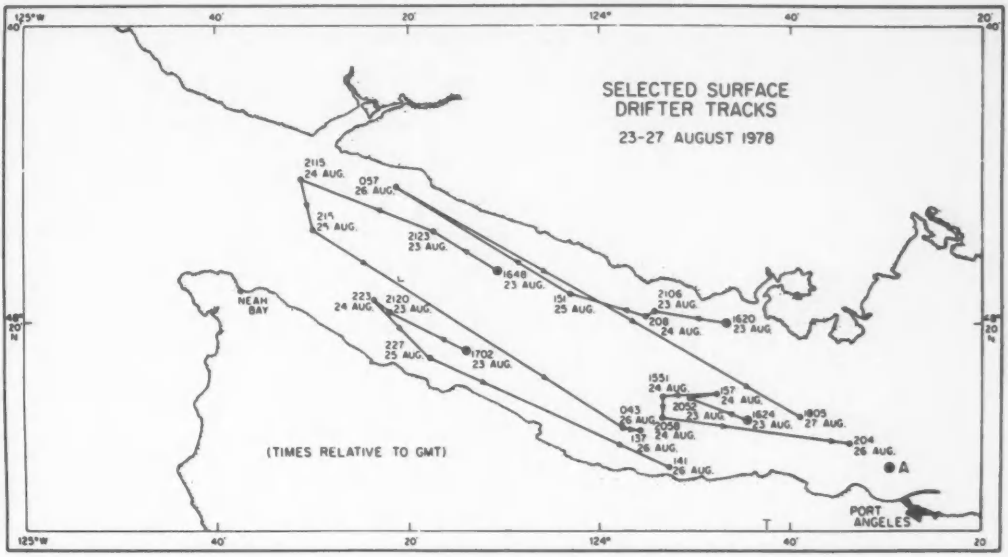


FIG. 22. Surface drifter tracks showing a flow reversal event in the Strait of Juan de Fuca. (From Frisch et al. 1981)

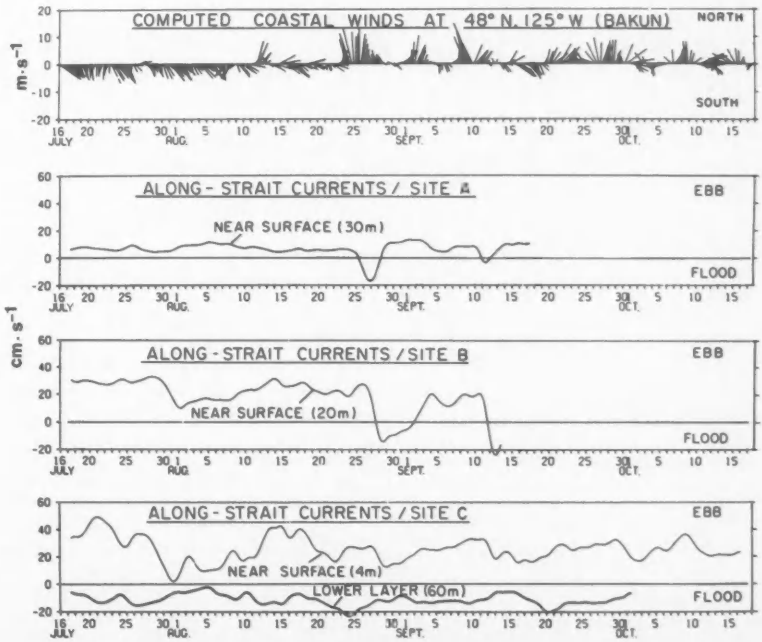


FIG. 23. Time series of daily averaged (1978) coastal winds and along-strait currents at three moorings in the Strait of Juan de Fuca, spanning the time of occurrence of the flow reversals of Fig. 18. Site A is shown in Fig. 22; sites B and C are a few kilometres east of it. Surface current reversals are clearly associated with southerly winds off the coast. (From Frisch et al. 1981)

To summarize, it would seem that there are practical as well as fundamental problems in determining the net rate of exchange between the Strait of Georgia and the Pacific Ocean. On a short time scale of a few days, the volume exchange may change sign as the result of offshore meteorological conditions. Even for longer time scales, over which fluctuations may average out, it may be difficult to achieve a high enough accuracy with moored current meter arrays to resolve the net transport.

Modeling

The construction of simplified conceptual models to represent the complexity of nature is a fundamental activity of science. Models are couched in terms of quantitative rules relating the values of measurable properties of nature. The consequences of these rules may then be explored with the tools of logic and mathematics to assess the pertinence of the rules themselves and to apply the model to unfamiliar situations. What distinguishes science as a method of describing nature is of course not the degree of sophistication of mathematical or numerical methods used, but its insistence on verification: the validity of the basic rules rests on their success in explaining ever-more-complicated situations.

Models are then used in two modes: as a method of testing hypotheses and as a predictive machine. The aim of the scientist is to develop a working model, testing it in the first mode, for the engineer to apply it in the second. Testing the ability of models to explain complex geophysical situations requires a level of description and understanding of which physical oceanography is just now becoming capable. What is required is not a mere identification of possible causes or a calculation of how some plausible mechanism might account for the observations, but rather a quantitative assessment of the role played by all possible mechanisms and recognition of their individual as well as collective effects in the observed property fields.

Although models of the physical oceanography of the Strait of Georgia have been developed with ultimate practical applications in mind, their formulation and verification have helped in clarifying the dynamics of flow interactions in the Strait. In reviewing these models, I shall try to assess the degree to which they are approaching the engineering level as well as the contributions they have made to the exploration of the dynamics of the Strait. It will be convenient to review separately the models of high-frequency processes (tides, upper layer) and those of long-period variability (deepwater renewal).

High-Frequency Models

Tidal models have already been mentioned in The Tides. The finite difference models developed by Crean (1976, 1978) have been well verified in their ability to reproduce and predict tidal sea level and current variations. This work has almost reached the engineering level but may still require some refinements in resolution to be applied on a small scale to specific areas. I have discussed in The Tides some of the improvements to model specification and output that I feel should be effected to turn the results of tidal models into reliable forcing functions for the study of low-frequency motions.

The upper layer model developed by Stronach (1977, 1981) has been mentioned in Estuarine Conditions, with an example of output shown in Fig. 10. The model integrates in time and space the equations of motion and continuity for a superficial layer of low-density water spreading over the Strait. Entrainement of salty water from below as well as dissipative effects are based on reasonable but rough parameterizations. The model structure cannot accommodate fronts, perhaps a difficult but probably a very important task. Its response to wind forcing has also not been tested. The model is thus still far removed from its practical goal of predicting upper layer motion for the use of oil spill tracking or marine rescue. Work continues (Stronach 1981) on model development as well as on the acquisition of data for calibration and verification. This model is thus still at that stage where its development serves as a focus for the study of the interplay between tide, winds, and runoff in the dynamics of the upper layer.

Predictive modeling of upper layer conditions in the Strait of Georgia is a problem very similar to that of short-term weather prediction: even with perfect knowledge of all physical phenomena, the task remains formidable. An array of rapidly reporting meteorological, runoff, and oceanographic monitors must be disposed in a carefully arranged manner so as to provide continuously updated forcing and boundary conditions. Powerful and reliable numerical techniques then must carry on temporal extrapolation on a scale of a few hours, or days. The complexity and cost of the process depend critically on the spatial resolution derived as well as on the nature of the prediction envisaged. It may well be that a model that accounts for property distributions and tracks fronts might not be realizable for a long time, while a simpler one, which attempts merely to represent surface displacements, could be put to use in the near future.

Low-Frequency Models

If high-frequency modeling is similar to weather prediction, low-frequency models are more akin to climate models: both low-frequency forcing as well as the integrated, rectified effects of more rapid fluctuations are to be brought together in a set of rules that allows calculation of future states. Our review of low-frequency phenomena — deepwater renewal, residual flows, oceanic exchanges — has shown that we do not know these rules. There are no models of long-period variations in the state of the waters of the Strait of Georgia beyond the qualitative ideas embodied in sketches such as Fig. 15 or in vague discussions of geostrophic turbulence. Unraveling of the long-term variability in the Strait of Georgia will remain a fundamental research problem for many years to come; the observations are sparse and the basic mechanisms are very poorly understood. However, it is difficult to imagine how any progress will be made unless serious and continued intellectual effort is expended on quantitative modeling of the system.

Any model of long-period phenomena in the Strait of Georgia, be it based on the theory of geophysical fluid dynamics or on empirical statistics, must explain deepwater replace-

ment in terms of all possible forcing inputs; Crean's laterally averaged model shown in Fig. 17 is a first step in that direction. In addition, the nature of the observed low-frequency variability, its distribution in time and space, the source of its energy, and its relation with the water renewal process must be explained. Under present conditions, when we can do none of the above, long-term planning should take at least as much account of our ignorance as of what little we have learned from observations. Management from a position of ignorance is an extremely difficult practice and I shall now discuss how the situation might be improved by further research.

Future Research

There is still obviously much more research to be done on the physical oceanography of the Strait of Georgia. My previous discussion of present modeling capabilities suggests a number of avenues along which future research should focus.

The high-frequency phenomena, particularly the tides, are best understood and are nearest the level of engineering use. Although there are still a few points of physics that might warrant further study, especially in the specification of dissipation mechanisms, the task of refining tidal models towards operational use is not likely to excite the interest of physical oceanographers. There is, however, a definite need for further development and refinement of numerical tidal models; it is only after they have been used repeatedly and tested on smaller scales in a variety of local configurations that they will be used with a certain degree of confidence on an operational basis. A once successful model is like a once flown airplane in terms of the confidence it inspires. Further use and development of tidal models should now strongly be encouraged within the engineering community.

An enormous amount of basic as well as applied work remains to be done before upper layer modeling can be used at the operational level, i.e., in scenarios in which the Coast Guard or the Environmental Protection Service may dial it up in an emergency for information on the drift of boats in distress or of spilled oil. Although the model developed by Stronach (1977, 1981) embodies much of the physics of the upper layer dynamics (except for wind forcing), and although it yields some reasonable-looking flow patterns (cf. Fig. 10), it still includes a number of poorly tested parameterizations. Furthermore, that model has yet to be subjected to critical field verification. Because of the overlapping nature of many of the problem areas in upper layer modeling, research should proceed along a number of parallel paths. Basic physical studies on the parameterization of friction, entrainment, and boundary conditions should go hand in hand with further numerical model development, including the problem of incorporating fronts within the model. The collection of calibration and verification data should take place at the same time as the theoretical work. My earlier comment about the need for repeated testing and verification to establish confidence in the model applies with even greater emphasis in this case, which is much more complicated than the tides.

The observational requirements that accompany the development of the upper layer model present a challenging task to the field oceanographer. What is needed for a critical test of the model is a sequence of maps of flow and water properties at the surface of the Strait, supplemented by a few vertical profiles. It will of course not be possible to resolve time scales of a few hours as well as frontal scale spatial structures over the whole Strait with a shipborne sampling program. Satellite remote sensing techniques, which ideally lend themselves to high-resolution spatial surveys, will certainly have to be used. Shore-based radar measurements, either in the classical tracking mode or in their modern guise as a direct method of measuring currents (Barrick et al. 1977), should also be utilized. If there is a lesson to be learned from the recent development of oceanography, it is that old problems sometimes yield to new observational techniques. The search for original sampling methods as well as instrument development should thus be strongly encouraged in connection with the upper layer sampling problem.

The practical aims of upper layer modeling should also be subjected to critical scrutiny. The benefits of a reliable working upper layer model are immediately evident, and it would be tempting to strongly encourage its development with money and manpower. Because of the complexity of the problem (I have already alluded to the similarity with weather forecasting) a serious examination of just what is expected of a model should be carried out at an early stage. I believe that there are two distinct levels of operational capability. The first one is relatively simple; it uses current information on the wind, the discharge, and the tides, together with results from the upper layer model for that appropriate set of circumstances, to predict directions and speeds of surface drift. The model is not run for each application on demand; rather, it is run and verified once for a wide range of conditions, following which the results are stored to be consulted as needed in future times. Each application then consists of looking up the appropriate values within a result matrix. It seems reasonable to expect that this kind of model application might become possible, perhaps within a decade. The higher level of modeling, similar in nature to numerical weather prediction whereby a model is run perhaps on a daily basis with continually updated inputs, represents a vastly superior level of effort and puts extremely high demands on computational efficiency, physical accuracy, and data sources. It is difficult to imagine that this level of modeling would be applied in the Strait of Georgia within the foreseeable future. Practically oriented research should thus perhaps focus on development of a simpler model.

Certainly the most fundamental problems facing physical oceanography in the Strait of Georgia concern the nature and the mechanisms of deep residual flows and slow water exchange with the ocean. This is where the mysteries lie and where fundamental research is likely to focus in the years to come. The study of the structure and origin of the deep residual flow takes on universal relevance in the framework of geophysical fluid dynamics; there are obviously some important but not yet understood dynamic processes responsible for the presence of the observed low-frequency energy. The Strait of Georgia is a readily accessible and an already partly documented laboratory area for the study of processes that may be just as important in many other coastal basins, and the rewards of local research may far transcend the local scene.

The elucidation of the deep flow mechanisms in the Strait will require concerted theoretical and observational efforts.

The complexity of the situation recently revealed by observation indicates that future measurements will have to be carefully planned: the long periods and short spatial scales involved make exhaustive sampling impossible. Imaginative observational programs are necessary, guided by careful theoretical assessments. The feasibility of acoustic monitoring, a small-scale version of the tomographic scheme of Munk and Wunsch (1979), should perhaps be investigated for application in an area lacking a sound channel but of restricted dimensions. Acoustic Lagrangian tracking of deep floats might also provide a more global type of information, more in tune with the interests of those concerned with pollution and perhaps more indicative of the processes of deepwater replacement.

The bathymetry of the Strait of Georgia (cf. Fig.18) must play an important role in the vorticity balance and in steering deeper currents. Theoretical studies should attempt to model bottom features more accurately. In particular, a logical step in the study of slow current fluctuations of a basin would seem to be an examination of its free second-class modes of oscillation. Because of the steep slopes found in the Strait, one might expect vorticity modes to be trapped on specific features, in a manner similar to that found by Platzman et al. (1981) on an oceanic scale. Concentration of particular modes on specific sloping segments, with strong currents there but nowhere else in the basin, makes the basin response extremely dependent on the form of the forcing. In view of the possible importance of nonlinearity in the deep residual flows, fundamental studies of small-scale, slow flow interaction in steep-sided basins will be absolutely essential in understanding the energy balance of the deep residual flows. Finally, residual flow outputs of tidal models should eventually be applied to a realistic simulation of the low-frequency dynamics of the Strait to examine this possibly important forcing mechanism.

Deepwater renewal may well be related to the deep residual flow problem, and even though the two questions may be treated separately for convenience, their separability should remain under question. Monitoring of a deep central station in the Strait of Georgia should be continued, preferably on a monthly basis; this is the only source of data on interannual variability of the deep waters of the Strait. The presently available time series at station *Georgia 1* (Fig. 14) should be examined in some detail and correlated with other possibly related phenomena on which long-term information is available. A simple but careful parameterization of deepwater formation and oceanic exchange similar to that formulated by Welander (1974) for the Baltic might also provide a useful heuristic tool for studying long-term variability in the Strait of Georgia.

Conclusions

Great progress has been achieved in our understanding of oceanographic phenomena, in the Strait of Georgia as elsewhere, in the last quarter century. This progress has been at the level of individual features: fronts, tides, estuarine flow, internal waves, etc., but also, and most significantly, in the integration of our knowledge of the various subsystems into an organic whole. This review has described the principal flow components of the Strait of Georgia and discussed some of their interrelations. A reader in search of a definitive and intimate explanation of how all the parts fit together may, however, feel disappointed: much of the emphasis has been on those points where our ignorance is greatest. Those are of course at the focus of present and future research. Despite all the progress made, there are still some important and fundamental questions that we cannot answer concerning the dynamics of the Strait of Georgia. Some of these questions bear on the practical application of knowledge recently acquired, as in attempts to model the Fraser River plume; some others reach down to the level of basic physical processes, as in explaining the nature of residual flows and deepwater exchange. We do not know how the various wheels and valves of our fluid dynamical engine are actuated. To quote Henry Stommel (1982) in a similar context where he imagines trying to explain to a ship's engineer how the ocean works as a machine, "there is an immense discrepancy between knowing how a machine works and being in the early stages in exploring an unknown machine." These words apply just as well to the Strait of Georgia as to the ocean and in both cases (to quote Stommel), "despite a vast accumulated literature, our ignorance of how the ocean actually works is vaster still." This is the spirit in which I would like to close this review: the challenge of discovery and exploration remains as fascinating to us as to our predecessors of decades past.

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Review of the Biological Oceanography of the Strait of Georgia: Pelagic Environment[1]

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Different components of the food web in the Strait of Georgia are reviewed. The phytoplankton are dominated by diatoms; however, flagellates may dominate in the winter. Chlorophyll *a* concentrations may range from <1 mg·m^{-3} in the winter to >15 mg·m^{-3} during blooms. The average annual primary productivity is about 280 g C·m^{-2} for the strait, but it is higher in frontal areas at the north and south ends of the strait and near the Fraser River plume. Light limits primary productivity during the winter months, while nutrients (nitrogen) and grazing are the limiting factors during the late spring and summer. Turbidity and salinity effects occur near the Fraser River plume. The surface macrozooplankton community is composed chiefly of copepods. Mid- and deep-water communities consist of euphausiids, chaetognaths, and some deep-living copepods, which overwinter at depth. The standing stock of macrozooplankton (>350 μm) to 400 m, ranges from 0.1 to 2.0 g wet wt·m^{-3}. Few estimates of secondary production and standing stock estimates of microzooplankton have been made. Horizontal patches of zooplankton have been encountered and may be important feeding sites for some fish. Standing stock associations of the dominant species in the food web of the strait are reasonably well known, but assessment of food web dynamics from these limited standing stock measurements is often inaccurate. There is a noticeable absence of data on how rate processes affect standing stocks, and it is particularly an understanding of these interrelationships that is needed for fisheries management. There is an urgent need for more interaction between biological oceanographers and fisheries scientists, particularly in the area of zooplankton grazing by larval fish.

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Ce qui suit est une revue des diverses composantes du réseau alimentaire du détroit de Géorgie. Bien que le phytoplancton soit dominé par les diatomées, les flagellés peuvent être dominants en hiver. La gamme de concentrations de chlorophylle *a* peut aller de <1 mg·m^{-3} en hiver à >15 mg·m^{-3} pendant les floraisons. La productivité primaire annuelle moyenne est d'environ 280 g C·m^{-2} dans le détroit, mais est plus élevée dans les zones frontales des extrémités nord et sud du détroit et près du panache du fleuve Fraser. La communauté zooplanctonique de surface est composée surtout de copépodes. Celles des eaux moyennes et profondes consistent principalement en euphausides, chétognathes et certains copépodes d'eau profonde qui y passent l'hiver. La biomasse du macrozooplancton (>350 μm) jusqu'à une profondeur de 400 m varie entre 0,1 et 2,0 g de poids humide·m^{-3}. On a fait à ce jour peu d'estimations de production secondaire et de biomasse du microzooplancton. Des taches horizontales de zooplancton ont été observées et, pour certaines espèces de poissons, peuvent être d'importantes aires d'alimentation. On connaît assez bien les associations de biomasse

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des espèces dominantes dans le réseau alimentaire du détroit, mais l'évaluation de la dynamique de ce réseau à partir de mesures limitées de biomasse est souvent imprécise. Il y a un manque évident de données sur la manière dont les processus liés aux taux influent sur la biomasse, et on a grand besoin, pour la gestion des pêches, de mieux comprendre ces interrelations. Il y a également un urgent besoin de plus d'interactions entre océanographes biologistes et halieutistes, surtout dans le domaine du broutage des larves de poissons sur le zooplancton.

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THE Strait of Georgia is a partly enclosed basin on the west coast of Canada lying between the mountainous coast range of the mainland of British Columbia and the southern half of Vancouver Island. The strait comprises an area of 6900 km^2. It is a valuable fishery and rearing area for the young of several major stocks of Pacific salmon and for large stocks of herring. Therefore, it is important to have a comprehensive understanding of the biological oceanography of this economically important area. This review describes the pelagic food webs in the strait and factors affecting the production processes and expands past reviews (Parsons et al. 1970; Parsons 1979).

Geographic and Hydrographic Features of the Strait of Georgia and Associated Inlets

The strait can be viewed as a coastal basin with tributary inlets. It is connected to oceanic waters by complexes of narrow shallow channels, causing intense daily tidal mixing primarily at the northern and southern ends of the basin. Although the strait is temperate in climate, structure and circulation in the southern half of the strait is strongly affected by the large discharge of the Fraser River, particularly during the early summer snow and glacier melt from the British Columbia interior. The many other smaller streams and rivers produce local effects. We thus have a narrow basin intensely mixed at both ends, with a major point source of freshwater in the southern half.

The physical and chemical characteristics of the strait have been previously reviewed by Tully and Dodimead (1957), Waldichuk (1957), and more recently by Thomson (1981) and LeBlond (1983). Only a brief summary of the features that are important in understanding the biological oceanography of the strait will be presented here. The Strait of Georgia can be considered a positive estuary because precipitation plus runoff is greater than evaporation, and the net surface flow is seaward. It has access to the open Pacific Ocean through Juan de Fuca Strait in the south and through Johnstone and Queen Charlotte straits in the north; however, flow in and out of the basin is restricted by relatively shallow, narrow channels such as Rosario Strait in the south and Seymour Narrows in the north (Fig. 1). Its surface waters with a salinity in the central region of 24–32‰ are diluted by freshwater, and especially by the Fraser River, which affects surface currents in the southern half of the strait. Currents are affected by semidiurnal tidal pulses entering through Juan de Fuca and Johnstone straits and southeast winds, which are maximal in December and January. This results in a generally counterclockwise circulation pattern with the strongest currents along the mainland shore. However, as local current patterns are complex, frontal regions often occur off the Fraser River and near restricted passages such as Seymour Narrows in the north and Rosario Strait in the south. Turbulent mixing extends 10–15 km into the strait as the tide ebbs and flows through these passages at speeds up to 6 m·s^{-1} in the north and 2 m·s^{-1} in the south. The northern part of the strait is generally stratified in the summer due to the heating of the surface waters from 7 to 22°C, but it is mixed by the wind in the winter.

Stability in the southern part of the strait is generally more complex because of the seasonal influence of the Fraser River. The discharge from the river contributes up to 80% of the total land runoff, and when the river discharge is high in June, it forms a plume of silt-laden, brackish water, which can cover a large part of the southern strait. The plume generally moves northward along the eastern shore of the strait, but it may be blown southward by northeast winds. There is also some north–south oscillation due to tides. The stability is high near the mouth of the Fraser River due to the low salinity (<20‰) surface layer.

There are six well-developed inlets or fjords associated with the Strait of Georgia: Saanich Inlet, Burrard Inlet, Howe Sound, Jervis Inlet, Desolation and Pendrell sounds, and Bute Inlet. They vary in the amount of runoff that they receive, but all of them have a net seaward surface water flow. The hydrography of these inlets is discussed in detail by Pickard (1961) and LeBlond (1983). The first three inlets have been subject to extensive biological investigations, and therefore, a brief summary of their hydrographic features will be presented.

Saanich Inlet is the best studied of the inlets (Herlinveaux 1962). It is a fjord 24 km long and 230 m deep. There is a shallow sill at the mouth at 75 m. The deep water in the basin becomes anoxic, as only the upper 50–75 m is mixed. It is a low-runoff inlet because Goldstream River at the head of the inlet has a small discharge. Surface heating produces a shallow thermocline at 5–10 m and stable surface waters. The deep water of the inlet is usually flushed once a year when denser water from the Strait of Georgia flows over the sill and into the basin of the inlet. This is the main supply of the oxygen to the deep water in Saanich Inlet. The oxygen is usually depleted in a few months and the deep water returns to its anoxic condition for the remainder of the year. Burrard Inlet, composed of Vancouver Harbour, Indian Arm, and Port Moody Arm, is a fjord 22 km long and 200 m deep. It receives medium runoff from the Indian River and many small surrounding streams. Two sills at 15 and 18 m in Vancouver Harbour severely restrict deepwater exchange between Indian Arm and the Strait of Georgia. The outer section of Burrard

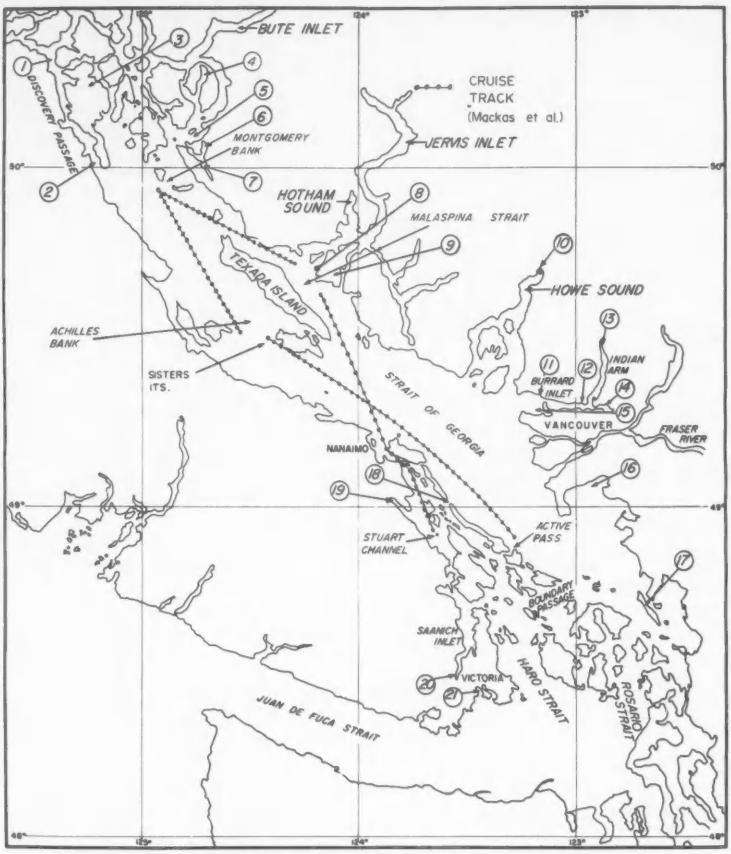

FIG. 1. The Strait of Georgia and contiguous waters. A cruise track is also shown for the zooplankton sampling and the data obtained in Fig. 7A, B, and C. Geographical locations referred to in the text are indicated by numbers. 1, Johnstone Strait; 2, Seymour Narrows; 3, Quadra Island; 4, Pendrell Sound; 5, Desolation Sound; 6, Theodosia Inlet; 7, Malaspina Inlet; 8, Hidden Basin; 9, Nelson Island; 10, Squamish River; 11, Capilano River; 12, Seymour River; 13, Indian River; 14, Port Moody Arm; 15, English Bay; 16, Boundary Bay; 17, Lummi Island; 18, Porlier Pass; 19, Ladysmith Harbour; 20, Goldstream River; 21, Esquimalt Lagoon. Beyond the chart to the north are the following: Dixon Entrance (north of Queen Charlotte Islands), Queen Charlotte Sound (northern end of Vancouver Island), Forward Harbour (off central Johnstone Strait), Knight Inlet (off central Johnstone Strait).

Inlet is influenced by the Capilano and Seymour Rivers, other small streams, and discharge from the Fraser River. During a large part of the phytoplankton growing season (June–September), silty Fraser River water greatly decreases light penetration in the surface layers. Further details of hydrographic aspects can be found in Gilmartin (1962, 1964), Stockner and Cliff (1979), and Davidson (1979).

Howe Sound is a relatively high runoff inlet due to the Squamish River discharge. From May to September the river carries a heavy glacial silt load, which forms an opaque, brackish surface layer that greatly restricts light penetration (Hoos and Vold 1975).

Phytoplankton

Records of marine diatoms from the region extend back to the nineteenth century, but these earliest records refer only to benthic species. The first study of the phytoplankton community provided a taxonomic list of diatoms from Departure Bay on the east coast of Vancouver Island (Bailey and MacKay 1916). Since then, more than 30 papers have described organismal aspects of the phytoplankton. There is additional information in several theses and unpublished reports cited here and in a recent bibliography of the area (Harrison et al. 1983). In the 1920's, several studies focused on the influence

of the Fraser River on the spatial distribution of diatoms (Lucas and Hutchinson 1927; Hutchinson 1928). In the following decade, work was concentrated at Friday Harbor Laboratories on San Juan Island and the Gulf Islands (e.g. Gran and Angst 1931; Gran and Thompson 1930; Johnston 1932; Phifer 1933, 1934). During the following 20-yr period (1940–60), relatively few phytoplankton studies were conducted. A resurgence of interest began in the early 1960's with studies in Indian Arm on primary productivity (Gilmartin 1964) and community structure (Buchanan 1966).

It is important to realize that prior to the 1960's nearly all the observations were restricted to "netplankton," which were greater than 20 μm in size or even larger depending on the type of netting used. Consequently, the "nanoplankton" (<20 μm) were usually completely missed or severly underestimated. Recent oceanographic research suggests that this <20 μm fraction may be a very important biomass component depending on the locale and time of year (McCarthy et al. 1974). Large variations in species lists or counts from the same geographical area by different investigators could be due to differences in the type of collecting gear (nets versus water bottles), preservatives or fixatives, depths sampled, and taxonomic identification skills of the investigator, thus obscuring any actual differences. While most netplankton can be readily identified by the use of the light microscope, there are some genera such as *Thalassiosira*, *Coscinodiscus*, and *Nitzschia* where a scanning electron microscope is essential for identification to the species level. Therefore, misidentification of species belonging to these genera is common in early records (Gran and Angst 1931; Cupp 1943). Many "naked" species do not preserve recognizably and therefore, they have undoubtedly been inadequately recorded.

Composition and Seasonal Changes

The phytoplankton of the Strait of Georgia and its adjacent waters is typical of cold temperate, coastal waters with some estuarine influence, including the latitudinal cosmopolitanism, which is characteristic of phytoplankton as a whole (Fig. 2A). Thus, for example, the community is almost identical to that found in Norwegian coastal waters (Braarud 1976), with the exception of a few species present in the Pacific but not in the Atlantic (see below). It is also similar to that found off eastern Canada (Gran and Braarud 1935; Brunel 1962), the west coast of Japan (Yamaji 1972), and the United States (Garrison 1979) and even similar to Southern Hemisphere waters such as Chile (Avaria and Orellana 1975) and the west coast of South Africa (Boden 1950).

Diatoms — Diatoms in the strait are represented by more than 200 taxa and dominate the size fraction greater than 20 μm throughout most of the year (Gran and Angst 1931; Légaré 1957; Buchanan 1966; Stockner and Cliff 1975, 1976, 1979; Stockner et al. 1975, 1979; Shim 1977a, 1977b; Fig. 2A). For illustrations of common diatoms of the strait, consult Cupp (1943); Gran and Angst (1931) may be useful in some cases. These two references should be brought up to date by consulting in Shim (1977a) and Hasle (1978). The most common species (frequency and biomass contribution) is *Skeletonema costatum*, a chain-forming centric diatom that is important in temperate coastal waters throughout the world. It usually accompanies, or closely follows, the spring bloom of *Thalassiosira* spp. (Stockner et al. 1979; Stockner and Cliff 1979), consisting largely of *T. nordenskioldii*, *T. aestivalis*, and *T. pacifica* (see Shim 1977a and Hasle 1978 for a discussion of these species, including material from British Columbia). These, in turn, are replaced by early summer *Chaetoceros* blooms (various species, of which *C. debilis* is usually the most abundant), *Ditylum brightwellii*, *Detonula pumila*, *Leptocylindrus danicus*, and species of *Nitzschia* (Takahashi et al. 1977: Stockner et al. 1979, Fig. 2B). *Cerataulina bergonii* and *Eucampia zoodiacus* may also form summer blooms, particularly in the central and southern strait. A few large *Coscinodiscus* spp. follow in the late fall as diatom numbers generally decline (Stockner et al. 1979; Fig. 2C).

Resting spores are frequently formed, particularly by *Chaetoceros* spp. (Hollibaugh et al. 1981) and occasionally by *L. danicus* (Davis et al. 1980) and *Thalassiosira* spp. Resting spores of *Chaetoceros* spp. may be important in forming the seed population for these summer blooms because after a short period of ripening in darkness at low temperature, resting spore germination rates can be quite high (Hollibaugh et al. 1981).

There is little indication that large salinity changes caused by the Fraser River discharge influence the composition of the diatom community. Shim (1977b) could recognize no brackish water diatom community in the plankton, although the presence of runoff was often marked by allochthonous freshwater species such as *Asterionella formosa*. He found that of a total of 219 diatom species, 29 freshwater species were introduced by the Fraser River or other rivers. A number of freshwater species were observed by Stockner et al. (1977) near the head of Howe Sound; these included *A. formosa*, *Hannaea arcus*, *Meridion circulare*, *Eunotia* sp., *Stauroneis* sp., and *Tabellaria flocculosa*.

Other intrusions into the region can also be recognized by the presence of particular diatom species. *Planktoniella sol* is a warm temperature to tropical diatom that has occasionally been recorded at depth in Juan de Fuca Strait, invariably in winter. Its appearance is presumably due to transport of open ocean water from the south by the Davidson Current, which enters Juan de Fuca Strait. A species that is common and endemic to the North Pacific oceanic region, *Denticulopsis seminae*, should be an excellent indicator of intrusions of oceanic, subarctic Pacific water (Taylor and Waters 1982). However, it has been observed only once in Jervis Inlet in summer (R. E. Waters, Department of Oceanography, University of British Columbia, Vancouver, unpublished observations).

Photosynthetic flagellates — Photosynthetic flagellates ("phytoflagellates") were first studied in some detail by Wailes (1939) who provided an early taxonomic guide to photosynthetic and nonphotosynthetic flagellates of this area. It is the best guide for this area, although its treatment of athecate (naked) dinoflagellates is inadequate. Since the phytoflagellates are composed of a number of algal groups (Chlorophyceae, Cryptophyceae, Chrysophyceae, Dinophyceae, Prasinophyceae, and Prymnesiophyceae) and they

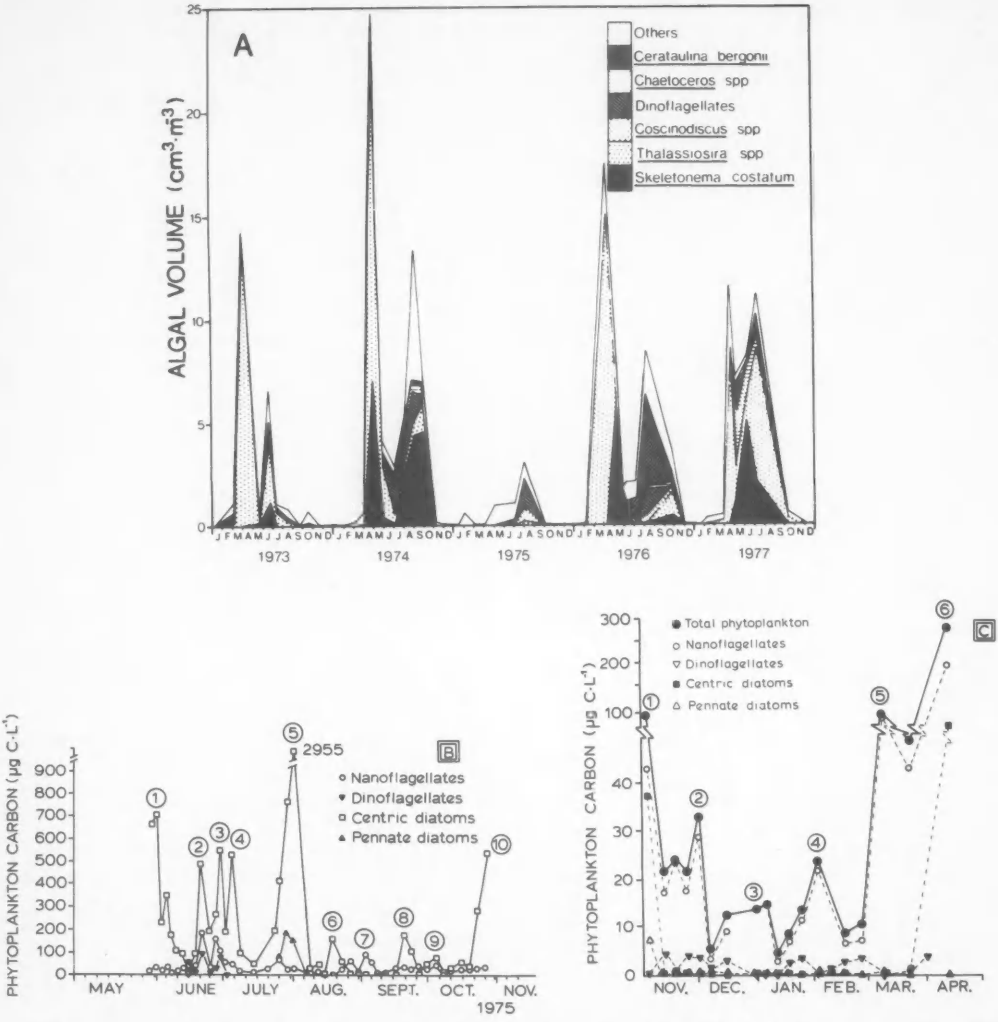
A
Others
Cerataulina bergonii
Chaetoceros spp
Dinoflagellates
Coscinodiscus spp
Thalassiosira spp
Skeletonema costatum
ALGAL VOLUME (cm³·m⁻³)
J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1973 1974 1975 1976 1977
B
2955
Nanoflagellates
Dinoflagellates
Centric diatoms
Pennate diatoms
PHYTOPLANKTON CARBON (µg C·L⁻¹)
MAY JUNE JULY AUG. SEPT. OCT. NOV.
1975
C
Total phytoplankton
Nanoflagellates
Dinoflagellates
Centric diatoms
Pennate diatoms
PHYTOPLANKTON CARBON (µg C·L⁻¹)
NOV. DEC. JAN. FEB. MAR. APR.

FIG. 2. The contribution of various phytoplankton groups to phytoplankton biomass. (A) During 1973–77 for boundary waters of the Strait of Georgia and Howe Sound for samples from 0 to 5 m (from Stockner et al. 1979). (B) During the summer of 1975 for Saanich Inlet for samples from 0 to 5 m. Encircled numbers indicate temporal increases in phytoplankton. ●, total phytoplankton; ○, nanoflagellates; ▽, dinoflagellates; □, centric diatoms; △, pennate diatoms (from Takahashi et al. 1977). (C) Same as Fig. 2B, except during the winter 1975–76 for Saanich Inlet for samples from 0 to 10 m. Note reduced scale on ordinate compared with Fig. 2B (from Takahashi et al. 1978).

are generally very small (<20 µm), they are very difficult to resolve taxonomically. Consequently, species identification by various investigators may vary considerably in their accuracy and detail.

Buchanan (1966) was the first to provide quantitative estimates of phytoflagellate abundance. He recorded 125 taxa, of which 88 were dinoflagellates (39 nonphotosynthetic). He found that cryptomonads, especially *Rhodomonas minuta*, were major contributors to the primary production of Indian Arm, particularly in late summer. Subsequently, Cattell (1969) focused on the distribution of dinoflagellates in the Strait of Georgia and their correlation with the concentration of vitamin B_{12}, known to be required by nearly all dinoflagellates tested. He found fewer dinoflagellate species (77) in the strait than Buchanan had found in the inlet, and a higher proportion (47 species) were nonphotosynthetic. In addition

to confirming the general pattern that dinoflagellates achieve greatest abundance in summer (he did not observe any "red water" blooms at his central strait stations), he discovered that gymnoid dinoflagellates contributed substantially to the spring bloom. For example, *Gymnodinium paulseni* reached 1.3×10^5 cells·L^{-1} in March 1967. Nonphotosynthetic species, such as *Protoperidinium* spp., are next to diatom blooms in abundance and they usually occur in early to mid-summer (F. J. R. Taylor, unpublished observations).

Some species such as the chrysomonad *Olisthodiscus luteus*, the photosynthetic ciliate *Mesodinium rubrum*, and the dinoflagellates *Gymnodinium sanguineum* (=*splendens*), *Noctiluca scintillans*, *Protogonyaulax* (=*Gonyaulax*) *acatenella*, *Protogonyaulax catenella*, and *Protogonyaulax tamarensis* may form dense blooms (Watanabe and Robinson 1979; Taylor 1975), which form "red tides" discoloring the water (see later section on red tides for more details). These three *Protogonyaulax* spp. are very closely related (Taylor 1975) and *P. acatenella* may simply be a form of *P. tamarensis* with greater flanges on its hypotheca. Even the distinction betwen *P. catenella* and *P. tamarensis* may be questionable, as morphological intermediates have been found. These two species differ in distribution, *P. catenella* occurring chiefly on the outer coast (up to 160 km offshore), in Juan de Fuca Strait (where it is particularly abundant in bays on the south side such as Sequim Bay), and into Puget Sound (Norris and Chew 1975; Taylor 1968). *Protogonyaulax tamarensis* occurs principally on the east side of the Strait of Georgia, from Lummi Island in the south to Nelson and Quadra Islands in the north. It is common in English Bay, Vancouver, in summer. The latter species clearly prefers water influenced by runoff; this is also the case in other regions, such as the Gulf of St. Lawrence or the Tamar Estuary in England. Populations with morphology intermediate between *P. catenella* and *P. tamarensis* have been observed in Saanich Inlet (R. E. Waters and F. J. R. Taylor, unpublished observations) and Boundary Bay (F. J. R. Taylor, unpublished obervations), localities that are also intermediate in geographical distribution. This aspect is under investigation at the time of writing. *Protogonyaulax* spp. appear to develop annually from benthic cysts (Turpin et al. 1978; Dobell 1978). Such cysts have been recovered from the sediments of Hidden Basin, Nelson Island, Theodosia Inlet, and Forward Harbour and they have been germinated in the laboratory (Dobell 1978). A survey of their abundance could provide information that may aid in bloom prediction.

Dinoflagellates can even be relatively abundant in the winter in Saanich Inlet, forming the second most dominant group after other nanoflagellates (Takahashi et al. 1978; Watanabe 1978; Fig. 2C). They were composed primarily of small dinoflagellates such as *Katodinium rotundatum* and *Gymnodinium* spp. In winter (November–March) nanoflagellates are the dominant group in Saanich Inlet composed of several cryptomonad genera, including *Cryptomonas*, *Chroomonas*, *Hemiselmis*, and *Plagioselmis*, prymnesiophytes such as *Dicrateria* and especially *Chrysochromulina kappa*, a prasinophyte *Pyramimonas*, and the chrysophyte *Apedinella* (Watanabe 1978; Takahashi et al. 1978; Fig. 2C). It is important to note that these latter two studies in Saanich Inlet are the only two detailed (weekly sampling) winter studies on phytoplankton community structure and distribution for the area. Consequently, they vividly illustrate that even in the winter, there are marked fluctuations in biomass over periods of a few weeks (Fig. 2C).

Silicoflagellates (Chrsyophyceae) such as *Ebria tripartita* and *Distephanus speculum* have been observed to occur in the strait in late summer and early fall (Stockner et al. 1979). In local areas they may be relatively abundant for short periods of time.

The smallest nanoplankters are less than 5 μm and consist chiefly of the prasinomonad flagellate *Micromonas pusilla* and coccoid green and blue-green algae. These are abundant to a depth of 100 m (F. J. R. Taylor, unpublished observations) or deeper, unlike the diatoms and flagellates, which are predominantly confined to the upper 20 or 50 m, or above the pycnocline. A virus has been observed to lyse *M. pusilla* in culture (Mayer and Taylor 1979), but it is unknown whether the distribution of this nanoflagellate is affected by viruses in nature. A brackish component is more evident in the phytoflagellates than in the diatoms. For example, the chrysomonad *O. luteus* and the dinoflagellate *P. tamarensis*, both known to prefer estuarine waters less than 15 or 20‰, seem to form blooms only on the east side of the strait on either side of the Fraser River plume (see "red tide" discussed under Pelagic–benthic (paralytic shellfish poisoning).

Recognition of the importance of ultraplankton (<5μm) has not been pursued in the Strait of Georgia. These algae, frequently consisting of very small flagellates and coccoid blue-green algae (Waterbury et al. 1979), are easily overlooked in preserved samples that are examined with a light microscope. Reports of high densities in other areas indicate that they may be an important food source for microzooplankton.

Photosynthetic ciliates — Ciliates are not usually considered to be phytoplankters. However, a few may be temporarily or permanently autotrophic due to symbiosis or retention of chloroplasts from their food (Taylor et al. 1971; Blackbourn et al. 1973; Oakley and Taylor 1978; Taylor 1982). *Mesodinium rubrum*, a highly modified gymnostome ciliate that contains an unusual cryptomonad symbiont, is an effective primary producer. Because of its strong swimming ability it can migrate vertically. Blooms of this ciliate are often subsurface and it can resist moderate downward flow, accumulating at convergences. *Mesodinium rubrum* is extremely widespread (Taylor et al. 1971) and is a successful exploiter of upwelled water. *Mesodinium rubrum* is a common cause of harmless red water in the area and may even bloom in winter.

Blackbourn et al. (1973) found that two other ciliates, *Prorodon* and *Strombidium*, can also retain chloroplasts from their algal food. The chloroplasts are remarkably intact when examined by electron microscopy and there is circumstantial evidence that suggests that they may continue to function for an unknown period after ingestion (F. J. R. Taylor, unpublished observations).

Geographic Influence on Species Composition

Most phytoplankton studies have focused on the southern or central Strait of Georgia. Data for the northern region,

other than the Pendrell Sound study (Stockner and Cliff 1975), are restricted to one earlier study (Stephens et al. 1969) and a series of samples collected from a small coastal tanker traveling through Dixon Entrance to the Queen Charlotte Islands (located north of Vancouver Island) (Perry et al. 1981). Despite the restrictions imposed by the collection methods (all samples from 3 m; track not repeated regularly), and the identification of taxa to the generic level in many cases, some general features can be detected. There appeared to be little change in composition within and north beyond the strait, with *S. costatum* being the dominant diatom in both areas. S. A. Cattell and F. J. R. Taylor (unpublished observations) found no obvious differences between summer samples taken at coastal localities in the Gulf of Alaska in 1966 and off the British Columbia coast. Perry et al. (1981) found that flagellates were numerically dominant in all their samples, which were collected primarily during late spring and summer.

The relative dominance of diatoms over other phytoplankters varies in different parts of the region. They are most abundant in the spring and early summer around the Fraser River plume and the entrances to the inlets, a trend reflected in the pattern of primary production. Lucas and Hutchinson (1927) found two zones of concentration associated with the plume; one was located at 11−12‰ and the other at 15−20‰. Stockner and Cliff (1976) found more diatoms at the entrance to Howe Sound than within it. It appears that medium to high runoff inlets favor flagellates more than diatoms, the same pattern being evident in Norwegian fjords such a Hardanger Fjord (Braarud 1976). On the other hand, low runoff inlets such as Saanich (Takahashi et al. 1977) or Hotham Sound (Stockner and Cliff 1975) support heavy diatom blooms, which can continue sporadically into the summer. Diatoms form a considerable part of the sediments in such locations. Very calm, stable conditions, which occur in Pendrell Sound (Stockner and Cliff 1975) or in protected bays, lead to the sinking of diatoms. These conditions also favor the development of flagellate blooms if nutrients are adequate, or aggregations of flagellates at the pycnocline if nutrients are poor.

Species composition, abundance, and timing of blooms may be influenced by areas of high turbulence such as Haro Strait (Stockner et al. 1979, see their Fig. 3B) or by turbidity of the water (Stockner and Cliff 1979, see their Fig. 4). In the latter case, the abundance and diversity of diatoms in Howe Sound was reduced at the head of the inlet, where turbidity was high compared with the mouth of the inlet. Effluent from Port Mellon and Woodfibre pulp mills drastically reduced the proportion of *Thalassiosira* spp. in the spring bloom, resulting in an almost unialgal bloom of *S. costatum*.

In summary, we have a basic understanding of the composition and distribution of phytoplankton in the central and southern Strait of Georgia; however, much of the information is based on lines of stations down the middle of the strait. There are indications that nearshore composition and abundance may be significantly different from the central part of the strait, and east and west sides may differ also. Therefore, there is a need for cross-strait sampling from shore to shore and a closer examination of subsurface and frontal concentrations using continuous profiling. Phytoplankton composition and distribution in the northern strait is poorly known, although some areas are evidently highly productive (Parsons et al. 1981b).

Standing Stock and Primary Production

Standing stock — The horizontal distribution of phytoplankton standing stock has generally been obtained by discrete point samples for chlorophyll fluorescence, or by frequent continuous sampling from a depth of approximately 2 m using a flow-through fluorometer (Stephens 1968; Parsons et al. 1970; Mackas et al. 1980; Parsons et al. 1981b; Fig. 3A). Recently, airborne estimates of surface (top 2−3 m) chlorophyll *a* have been obtained with a color spectrometer. This provides a measure of upwelling in vivo chlorophyll *a* fluorescence as a visible Gaussian line at 685 nm (Gower 1980; Parson et al. 1981b) and gives an instantaneous coverage of 2 by 100 m of sea surface. Results between comparisons of airborne and shipborne chlorophyll *a* estimates are very encouraging (Parsons et al. 1981b).

Generally, chlorophyll *a* concentrations range from <1 mg·m^{-3} in the winter (Fig. 3B) to >15 mg·m^{-3} during spring or early summer blooms (Stockner et al. 1979; Parsons et al. 1981b). Recently, a more detailed survey in July and August has shown that in frontal regions, where mixing is high, there are areas of high chlorophyll *a* concentrations (from 3 to >5 μg·L^{-1}), particularly at the northern end of the strait (Fig. 3A). The most marked changes in chlorophyll *a* occur in the vicinity of the Fraser River plume and these concentrations exhibit considerable lateral movement, even during a single tidal cycle (Parsons et al. 1969b). Seasonal variations also occur in the vertical distribution of chlorophyll (Fig. 4A), and a prominent deep chlorophyll maximum frequently occurs in the summer (Parsons et al. 1970).

Patterns in chlorophyll concentrations similar to those in the strait occur in the inlets such as Saanich (Takahashi et al. 1977, 1978) and Howe Sound (Stockner and Cliff 1979). Takahashi et al. (1977, 1978) have shown rapid, temporal fluctuations in chlorophyll concentration in Saanich Inlet through weekly and biweekly sampling. In addition, they frequently observed a well-developed, subsurface chlorophyll maximum near the pycnocline at 5−8 m, after the spring diatom bloom sank due to nutrient exhaustion (Takahashi et al. 1977, 1978, see their Fig. 13).

Other estimates of phytoplankton standing stock have included cell numbers and volumes (Stockner et al. 1977, 1979; Takahashi et al. 1978; Fig. 2A). Cell numbers and appropriate species identification have the advantage of giving estimates of the contributions of various species relative to the total community. However, the conversion of cell numbers and volumes into carbon is not quantitative because some cellular shapes are poorly represented by certain geometrical shapes and corrections for vacuolar volumes are only approximate. Such a calculation has been made for Saanich Inlet and clear trends are evident (Fig. 2B, and C). For example, even though nanoflagellates form the dominant biomass in the winter, they constitute only 10% of phytoplankton carbon observed during the spring and summer months, despite the fact that they may be relatively numerically important. Seasonal variations in other standing stock parameters such as seston, particulate

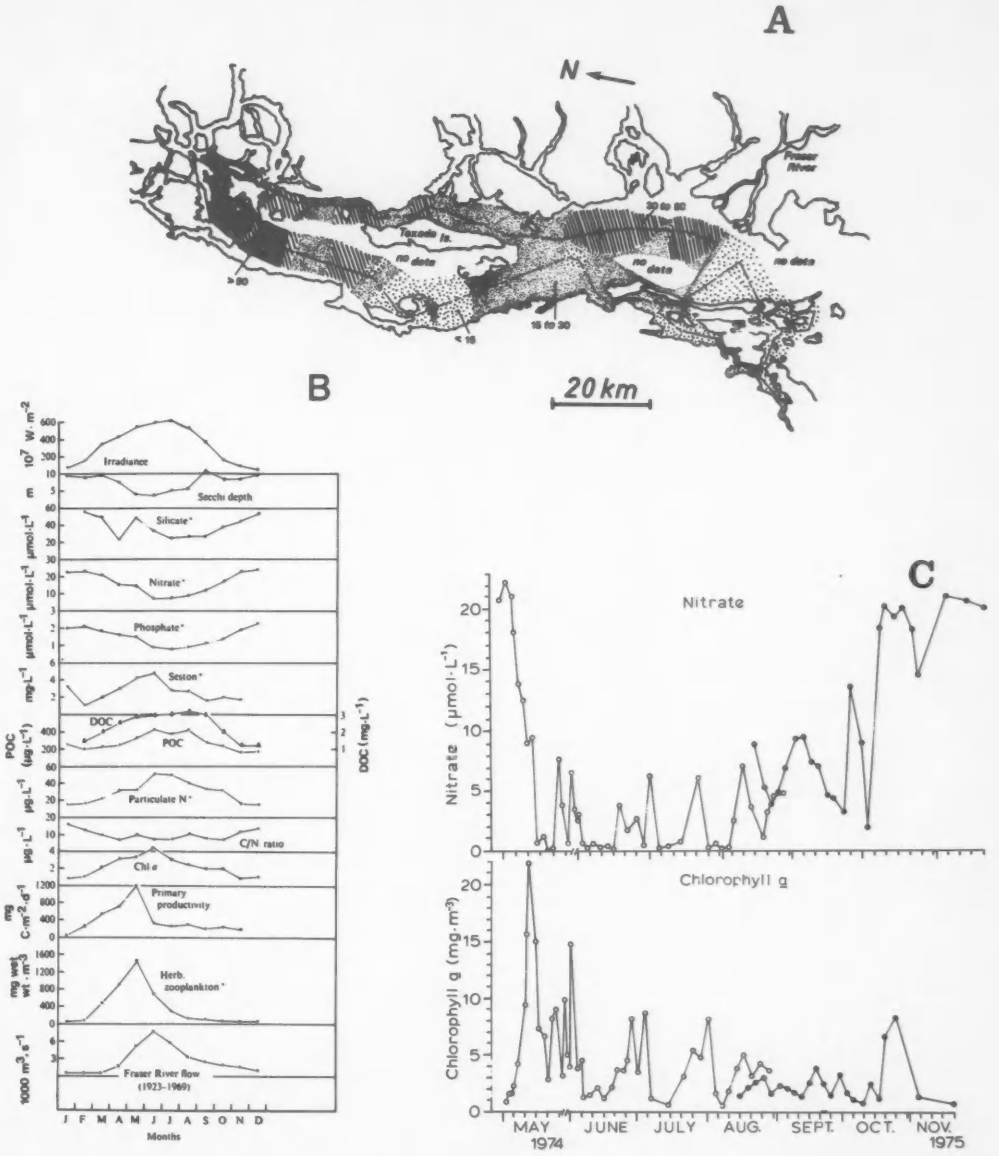

FIG. 3. Temporal and spatial variations in phytoplankton standing stock. (A) Contours of in vivo chlorophyll fluorescence determined by continuous fluorescence measurements from the cruise track during the summer (June 28–August 2, 1980) in the Strait of Georgia. To obtain approximate values of chlorophyll *a* in micrograms per litre, divide fluorescence values by 10 (from Parsons et al. 1981b). (B) Seasonal cycle in physical and chemical parameters, standing stock, and productivity expressed as monthly averages for the period 1965–68 for the Strait of Georgia (+ denotes average value for 0–20 m in the water column). DOC and POC represent dissolved and particulate organic carbon, respectively (from Parsons 1979). (C) Weekly changes in nitrate and in chlorophyll *a* in the water column (0–10 m) in Saanich Inlet at two closely spaced stations (● and ○) during the summer of 1975 (from Takahashi et al. 1977).

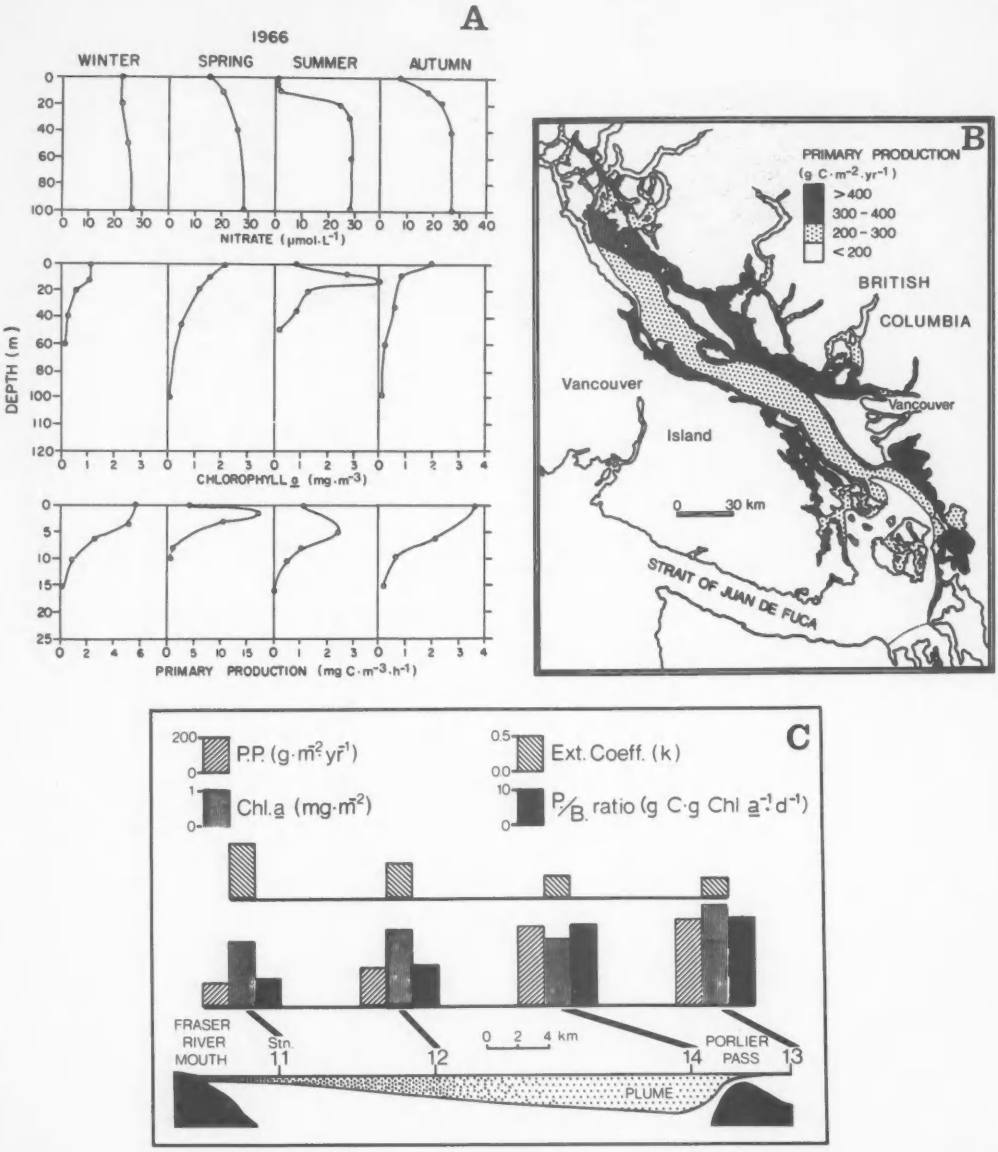

FIG. 4. Temporal and spatial changes in primary productivity in the Strait of Georgia. (A) Seasonal changes in the depth distribution of nitrate, chlorophyll *a*, and the primary production for 1966 (from Parsons et al. 1970). (B) Variations in annual primary productivity (from Stockner et al. 1979). (C) Schematic illustration of the impact of the Fraser River discharge on light attenuation and primary production. Histograms are mean 1976 values for stations on the east–west transect from the river mouth to inside Porlier Pass (from Stockner et al. 1979).

nitrogen, and particulate organic carbon are shown in Fig. 3B. These all follow the same general trend as chlorophyll *a*.

Primary production — Primary productivity data obtained over a 4 yr period (1965–68) for the strait show that

productivity begins to increase in February, reaches a maximum of 1.2 g $C \cdot m^{-2} \cdot d^{-1}$ in May, and then declines to 0.2 g $C \cdot m^{-2} \cdot d^{-1}$ in late summer (Fig. 3B; Parsons et al. 1970; Parsons 1979). Annual primary productivity was estimated to be 120 g $C \cdot m^{-2}$ (Parsons et al. 1970). Recently, estimates of annual productivity from a 2 yr study (1976–77) were about three times higher (approximately 345 g $C \cdot m^{-2}$) and occasionally, maximum daily productivity as high as 8 g $C \cdot m^{-2} \cdot d^{-1}$ was reported (Stockner et al. 1979).

Reasons for differences between these estimates of annual primary productivity have been discussed at length (Parsons et al. 1980; Stockner et al. 1980) and only a summary will be provided here. Five possible reasons are as follows.

1) Differences in ^{14}C methodology. Geiger counting of incorporated ^{14}C in desiccated algae on membrane filters was used to estimate ^{14}C uptake by Parsons et al. (1970). This method has been found to give lower estimates of primary productivity than the more recently available liquid scintillation counting technique. Differences in dark bottle corrections, irradiance, temperature, and incubation period may also have contributed to different productivity values.
2) Differences in frequency or distribution of vertical samples. Parsons et al. (1970) used point samples or integrated samples from 0.5, 10, and 20 m, while Stockner et al. (1979) used closely spaced point samples from depths of 0.5, 1, 2, 3, 5, 10, 20, and 30 m. Since a thin but pronounced chlorophyll maximum frequently forms in the summer just above the strongly developed pycnocline at 5–10 m (Fig. 4A), it is very easy to miss this important portion of the phytoplankton biomass by using predetermined sampling depths. A vertical profile of in vivo fluorescence obtained with an on-deck, flow-through fluorometer would be helpful to determine the vertical variability in biomass distribution. Alternatively, an integrated sample obtained by continuous pumping could be used.
3) Choice of stations. The rather large variation in annual primary productivity shown in Fig. 4B illustrates the importance and difficulty in choosing a small number of reference stations to represent the whole strait without apparent over or under bias. Ten of the 16 stations in the Stockner et al. (1979) study were within a 30-km radius of the Fraser River mouth, where productivity is known to be variable and frequently very high, especially in some of the back eddies. The northern section of the strait appears to have been undersampled by Stockner et al. (1979), since only four stations were used, all located towards the southern end of Texada Island. Two other stations on either side of Porlier Pass appear to have been associated with fronts, where continual upwelling from tidal activity resulted in enhanced productivity. While the 15 stations sampled by Parsons et al. (1970) may have been more evenly distributed over the strait, they were deficient in extent of seasonal coverage, since only 2 stations had more than four measurements in any year, or more than eight measurements in the entire 3-yr study (Stockner et al. 1980); the seasonal coverage in Stockner's study was not reported (Parsons et al. 1981b). The recent investigation of biological fronts in the strait has demonstrated the marked variation in chlorophyll distribuiton and revealed the difficulty in choosing appropriate, unbiased reference stations for a long-term study designed to determine annual primary production.
4) Method of calculating annual primary production. Annual primary production derived from integration of surface area production contours (Fig. 4B) gives a better estimate (a lower value, ~ 280 g $C \cdot m^{-2}$) than averaging the estimates from all the stations (345 g $C \cdot m^{-2}$; see Stockner et al. 1980, p. 1048).
5) Increased nitrogen input into the Fraser River from sewage. The diversion of sewage from Vancouver Harbour to the Fraser River has only increased the nutrient loading in the river from 5% in 1967 to 12% in 1977 (Clark and Drinnan 1980) and therefore, sewage would be expected to make a very minor contribution to increased primary productivity. The contribution of sewage to the total nitrogen concentration of the river is, to a minor extent, controlled by the discharge volume of the river for that particular year.

The only inlets for which annual primary production has been determined are Howe Sound (Stockner et al. 1977) and Burrard Inlet (Stockner and Cliff 1979). There was considerable variation between two consecutive years (300 and 516 g $C \cdot m^{-2}$ for 1973 and 1974, respectively) for a station at the outer edge of Howe Sound. The mean of these two years, 408 g $C \cdot m^{-2} \cdot yr^{-1}$, is somewhat higher than the mean value of 345 g $C \cdot m^{-2} \cdot yr^{-1}$ observed for the strait by Stockner et al. (1979). The annual primary production for stations near the head of the inlet was considerably reduced due to turbidity. Productivity at stations near Woodfibre and Port Mellon pulp mills was also lower due to significant discoloration of the water by effluent from the mills. When the annual primary production for all 10 stations sampled in Howe Sound was averaged, values varied from 118 to 163 g $C \cdot m^{-2} \cdot yr^{-1}$ for 1973 and 1974, respectively.

In Burrard Inlet, maximum values of primary productivity (532 g $C \cdot m^{-2} \cdot yr^{-1}$) occurred in Port Moody Arm, while the lowest values (260 g $C \cdot m^{-2} \cdot yr^{-1}$) occurred in Indian Arm (Stockner and Cliff 1979). This latter value is considerably lower than the mean of 455 g $C \cdot m^{-2} \cdot yr^{-1}$ calculated from measurements in Indian Arm by Gilmartin (1964).

Primary production in Saanich Inlet is spatially and temporally variable. Annual production was estimated to be about 250 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1975 (November 1974–August 1975) and about 500 g $C \cdot m^{-2} \cdot yr^{-1}$ in 1976 (March 76–October 76) (L. A. Hobson, Department of Biology, University of Victoria, Victoria, B.C., personal communication). These estimates are based on a 24-h in situ ^{14}C incubation at one station (mid-fjord), with a sampling frequency of once every 3 wk for the time period given in parentheses above. The maximum photosynthetic rate varied seasonally from about 0.5 to 1 mg $C \cdot mg\ chl\ a^{-1} \cdot h^{-1}$ for the winter to a maximum of 5–6 mg $C \cdot mg\ chl\ a^{-1} \cdot h^{-1}$ for June and July (Hobson 1981). Integrated daily photosynthetic rates varied from 5 to 60 mg $C \cdot m^{-2} \cdot d^{-1}$ in the winter (Takahashi et al. 1978) to about 4 g $C \cdot m^{-2} \cdot d^{-1}$ during the spring bloom.

In summary, a reasonable estimate of annual primary productivity in the strait is 280 g $C \cdot m^{-2}$. It is markedly higher than the open North Pacific Ocean, which varies from 60 to 100 g $C \cdot m^{-2} \cdot yr^{-1}$ (Hobson 1980b); however, it may not be too high when one considers adjacent waters where productivity was estimated to be 275 g $C \cdot m^{-2} \cdot yr^{-1}$ for the

southern part of Puget Sound, or 465 g $C \cdot m^{-2} \cdot yr^{-1}$ for the central basin of Puget Sound (Winter et al. 1975). It is a very expensive task to estimate annual primary productivity for a large area such as the strait where temporal and spatial (horizontal and vertical) variability is great. It may be more valuable if future field programs considerably reduced their area of coverage. This could be accomplished by focusing on highly productive areas such as fronts that are probably very important to the fisheries in the strait, rather than by trying to sharpen the estimate of annual primary productivity (i.e. information about the temporal and spatial variation may be more valuable than the mean of these variations).

Factors Affecting Standing Stock and Primary Production

Light and turbidity — Photosynthetically active radiation (400–700 nm) varies from a minimum of about 70 $W \cdot m^{-2}$ on a rainy day in December or January to a maximum of approximately 1400 $W \cdot m^{-2}$ on a bright sunny day in June (Fig. 3B). Therefore, for a period of approximately 5 mo (October–February), when irradiance is less than 200 $W \cdot m^{-2}$, primary production at the surface may be light limited and ranges from 0.2 to 0.4 g $C \cdot m^{-2} \cdot d^{-1}$ (Parsons 1979; Fig. 3B). During the remainder of the year, light may limit production during extended periods of cloudy weather (Takahashi et al. 1978, see their Fig. 11), or in specific areas where silt-laden river discharge may form an extensive, opaque, freshwater surface layer or plume, resulting in a marked increase in light extinction (Fig. 4C). Mean extinction coefficients have been found to range from 0.11 $\cdot m^{-1}$ in the winter to 2.90 $\cdot m^{-1}$ in the turbid water near the Fraser River during the spring freshet, which usually lasts from June to September (Stockner et al. 1979; Fig. 4C). Similarly, in Howe Sound the Squamish River discharge increased light extinction by almost one order of magnitude, and estimates from a simulation model indicated that turbidity decreased annual primary productivity by about 35% (Stockner et al. 1977).

Specific experiments demonstrating light limitation during the winter have been carried out for Saanich Inlet (Takahashi et al. 1978; Watanabe 1978). A water sample taken from 0- to 5-m depth was incubated at two different irradiances (1.5 to 150 $W \cdot m^{-2}$) in the laboratory and growth rate of various cell sizes was followed (Takahashi et al. 1978). After a 2-d lag, all cells growing under high light began to grow exponentially, with the larger cells (chain-forming centric diatoms such as *Chaetoceros* spp., *Thalassiosira* spp., and *S. costatum)* growing much faster than the small ones. Under low light, the opposite trend occurred, with smaller cells (nanoflagellates) growing faster than larger ones (Takahashi et al. 1978, see their Fig. 12). This light limitation effect is further enhanced by other winter conditions such as a very short photoperiod (9 h light:15 h dark), a high number of overcast days (25 or more per month), and a deep mixed surface layer due to strong winds. Thus, flagellates may dominate in the winter by maintaining themselves in the upper few metres by phototaxis (Watanabe 1978) and by having a lower compensation irradiance (Takahashi et al. 1978). In addition, assimilation of dissolved organic nitrogen and phosphorus compounds in dim light may be important for common winter flagellates such as *C. kappa* in Saanich Inlet (Watanabe 1978). During the winter it has been suggested that diatoms and dinoflagellates may be present as dormant cells or resting spores (Hobson 1981). This dormancy may be broken by a daily threshold irradiance, achieved primarily through an increase in day length from 12.8 to 13.5 h. Similarly , the onset of dormancy in the fall may occur when the day length decreases from 14.1 to 12.6 h. These ranges in daylength correspond to a mean irradiance of 149 to 170 $W \cdot m^{-2}$. In the Strait of Georgia, Stockner et al. (1979) found that the spring bloom began to develop at an irradiance of about 100 $W \cdot m^{-2}$.

In Howe Sound, lower irradiance values in the spring of 1974 delayed the spring bloom and *S. costatum*, rather than a *Thalassiosira* sp., dominated the phytoplankton (Stockner et al. 1979). This observation suggests that interaction between irradiance and temperature may be important in determining the species composition of the spring bloom.

Photosynthetic rates may be reduced due to photoinhibition, especially during sunny weather near midday for near-surface winter populations growing at 3–6°C (Takahashi et al. 1973, 1978). This photoinhibition may be temporary as cells adjust in a few days from cloudy to sunny conditions while growing at very low temperatures. During the summer under nutrient-limited conditions, cells may also show photoinhibition near midday (Takahashi et al. 1973).

Nutrients — Ambient nutrient concentration, in addition to grazing and light, is an important factor affecting primary production and regulating standing stock. All nutrients appear to be saturating except for a short period during the late spring and summer (May–September) when nitrogen may be limiting. While phosphate may also drop to low concentrations (0.1 $\mu mol \cdot L^{-1}$; see Takahashi et al. 1973), it is rapidly regenerated (Antia et al. 1963) and it is therefore generally regarded not to be rate limiting. Silicate has been observed to drop to approximately 1 $\mu mol \cdot L^{-1}$ for brief periods of time during the summer in Saanich Inlet (Takahashi et al. 1978, see their Fig. 5B). According to laboratory experiments, this concentration should reduce primary productivity for many diatom species (Paasche 1973) and may enhance their sinking rates (Bienfang et al. 1982). This has not been confirmed in field experiments for the strait, but multiple regression analysis for field data showed a correlation between ambient silicate concentration and maximum photosynthetic rate (Hobson 1980a, 1981).

Nitrogen has recently received attention with respect to its role in regulating primary productivity in the Strait of Georgia and attempts have been made to compose a nitrogen budget for the strait (Parsons et al. 1980; Stockner et al. 1980). As discussed earlier an average annual primary productivity for the strait of 280 g $C \cdot m^{-2}$ has been reported (Stockner et al. 1980), which is about two and a half times higher than previous reports of 120 g $C \cdot m^{-2}$ (Parsons et al. 1970). Discussion has centered on whether the sources of nitrogen are adequate to meet the nitrogen requirements for primary production of this magnitude. If one assumes that the C:N ratio for phytoplankton varies from 7:1 to 15:1 and the primary productivity is 280 g $C \cdot m^{-2}$ (based on integrating surface

area contours rather than averaging estimates from different stations), then the nitrogen requirement is 19–40 g $N \cdot m^{-2} \cdot yr^{-1}$ (Parsons et al. 1980). Based on calculations by Parsons et al. (1980, p. 1044), if surface waters (0–10 m) were depleted of nitrate (26 $\mu mol \cdot L^{-1}$), this would provide 3.64 g $N \cdot m^{-2} \cdot yr^{-1}$ or approximately 9–19%. In addition, nitrogen (nitrate plus Kjeldahl nitrogen) from the Fraser River was estimated from data by Hall et al. (1974) to supply 4.48 g $N \cdot m^{-2} \cdot yr^{-1}$ or approximately 11–23.5%. Assuming on an arbitrary basis that both these sources were recycled (reused) twice during the year, this would give a total nitrogen supply of approximately 16 g $N \cdot m^{-2} \cdot yr^{-1}$ ((3.64 + 4.48) × 2) or approximately 40–84%. This would leave an "apparent" shortfall of 3–24 g $N \cdot m^{-2} \cdot yr^{-1}$ or about 16–60%, depending on the C:N ratio used. However, this "apparent" nitrogen deficit could be made up by considering other sources, possibly in the following order: (1) entrainment of nutrient-rich deep water as the freshwater river discharge moves seaward at the surface, (2) wind mixing, (3) tidal mixing in turbulent passages, (4) increased nitrogen recycling from only twice to three times, (5) organic nitrogen sources (e.g. urea, amino acids, etc.) not included in the above calculations, (6) input from marshes and sediments in shallow areas, (7) input from terrestrial runoff and other rivers, and (8) vertical diffusion. A small contribution from several or all of these possibilities could easily supply the 7–30 g $N \cdot m^{-2} \cdot yr^{-1}$ required to balance the nitrogen budget.

At present, the contribution due to vertical entrainment as a result of river flow is uncertain. It is generally assumed that nitrate-rich water (approximately 25 $\mu mol \cdot L^{-1}$) is entrained into the surface layers; however, this may not be true during summer months when the entrained water may actually be relatively nitrate poor (Stronach 1977). If nutrient-rich water is entrained, then using a ratio of vertical entrainment flux to river flow flux of approximately 5:1, the vertical flux would contribute five times more nitrogen than the river, assuming equal nitrate concentrations in the river water and the deep entrained water (Stronach 1977). Therefore, vertical entrainment at the mouth of the Fraser River is potentially a very important nitrate source and it could conceivably make up the entire shortfall by itself.

Sources of organic nitrogen have not been included in nitrogen budgets for the Strait of Georgia, although they have been included in the river source via the Kjeldahl measurements. Urea, amino acids, and even purines such as hypoxanthine have been shown to be good sources for a large number of phytoplankton species (Antia et al. 1975). Furthermore, recycling of just one of these organic nitrogen sources, urea, has been shown to contribute up to 28% of the nitrogen required for primary productivity in another temperate estuary, Chesapeake Bay (McCarthy et al. 1977). This information indicates that there is an important need for determining the contribution of organic nutrient compounds to bacterial and primary production in the strait. The measurement of the horizontal and vertical distribution of key compounds such as urea and some amino acids would be an important starting point. Measurements of uptake rates of these compounds under a variety of ecological conditions by natural phytoplankton and bacterial populations would follow.

The importance of wind mixing and tidal mixing in relation to nutrient enrichment have not been qualified. The effects of mixing through Johnstone and Haro straits can be seen through increased chlorophyll concentrations in the summer, up to 10 km into the strait. It is also important to note that while tidal mixing may not be large, it does occur daily.

As a first approximation, nitrogen from the Fraser River can be a significant source, up to 30%, of the total available nitrogen for phytoplankton in the Strait. Increased loading of nitrogen in the Fraser River, owing to the rapid population growth (approximately 50%) in the area and the diversion of sewage from Burrard Inlet to the Fraser River, has been proposed as an important additional nitrogen source to the river (Stockner et al. 1979, 1980). However, Clark and Drinnan (1980) stated that recent estimates of annual nitrogen loadings to the Fraser River from Vancouver sewage effluents are small (5–12%) compared with upstream nitrogen sources. Variation in spatial and temporal factors, such as large seasonal or yearly differences in river discharge, makes comparisons of presewage and postsewage data difficult. For example, even though the contribution from sewage had substantially increased in 1977, the total nitrogen loading was actually less in 1977 than in 1967 because of the lower river discharge (3300 $m^3 \cdot s^{-1}$ in 1966 versus 4000 $m^3 \cdot s^{-1}$ in 1977; Clark and Drinnan 1980). Therefore, it is thought that sewage makes a small contribution to the nitrogen of the river, possibly up to 10%.

Seasonal trends in nutrient concentrations in the river have been observed, with highest values during the low flow period of January–March and decreasing values through the freshet (June) to a late summer minimum (Drinnan and Clark 1980, see their Fig. 22, 24, and 28). The low summer values are probably the combined result of dilution plus biological utilization, since minimum levels occur after the peak flow period. Summer minima and winter maxima are 1–4 $\mu mol \cdot L^{-1}$ for ammonium, 2–15 $\mu mol \cdot L^{-1}$ for nitrate, and 0.01–0.3 $\mu mol \cdot L^{-1}$ for phosphate. Silicate concentrations in the river are very high (100–200 $\mu mol \cdot L^{-1}$) and show less of a seasonal trend.

Saanich Inlet is the most intensively studied of the inlets with respect to nutrient budgets. An attempt has been made to draw up a nitrogen budget for this inlet, primarily for the spring and summer periods (L. J. Alexander, Department of Biology, University of Victoria, unpublished results; K. P. Guest, Department of Biology, University of Victoria, unpublished results). The concentrations of nutrients and the seasonal pattern of production and utilization are very similar to the strait. Minor differences appear because Saanich Inlet is a low runoff inlet and therefore, the contribution from vertical entrainment due to river surface flow is much less. The contribution of nitrogen from rivers (Cowichan, Goldstream and Fraser), runoff, and rain is unexpectedly high (up to 49%), since river discharge volume is low. Excretion of ammonium by *Euphausia pacifica* was estimated to be two times greater than bacterial regeneration (L. P. Alexander, Department of Biology, University of Victoria, unpublished results). Weekly and biweekly sampling by Takahashi et al. (1977) revealed that nutrient concentrations did not remain continually low over the summer. Nitrate concentrations rose and fell several times from low or undetectable levels to over 5 $\mu mol \cdot L^{-1}$ during the late spring and summer period due

to mixing by tides and/or winds (Fig. 3C). In addition to introducing nutrients into the euphotic zone, phytoplankton "seed" stock may also be introduced by mixing, giving rise to frequent summer blooms lasting a few days to 2 wk (Fig. 2C). This important study vividly demonstrates the misleading view of phytoplankton nutrient dynamics that would be obtained by the more traditional monthly sampling schedule.

The only vitamin studied in any detail for its rate-limiting effect on phytoplankton growth is vitamin B_{12}. Cattell (1969) detected a significant relationship between dinoflagellates and vitamin B_{12} levels with periods of negative correlation (indicative of usage from a limited supply). On the other hand, Prakash and Taylor (1966) found that a bloom of the toxic dinoflagellate, *P. acatenella*, was coincident with very high B_{12} levels in Theodosia and Malaspina inlets (13 $ng \cdot L^{-1}$ (determined by T. R. Parsons)). Cattell (1973) reported that B_{12} levels were highest in winter, but were also high during peak river runoff, and there was a slight increase during the spring bloom.

Salinity — The Fraser River contributes from 50 to 80% of the total land runoff into the Strait of Georgia (Herlinveaux and Giovando 1969; Waldichuck 1957) and causes a variation in surface salinity from 0.5‰ at the surface near the river mouth during spring freshet to about 27‰ away from the freshwater influence in the winter. Since the Fraser River affects such a large part of the strait, it is surprising that the effects of salinity variations on primary productivity have never been thoroughly examined. As a rule, primary productivity is considerably lower at the mouth of the river, but it is difficult (but not impossible) to separate salinity effects from decreased temperature (1 or 2°C). Further studies are needed to determine how a substantial increase in salinity affects the primary production of typical freshwater species in the river, such as *A. formosa*, and how a decrease in salinity affects marine species that might enter the river mouth by entrainment.

The primary productivity of the upper regions of Howe Sound is also significantly affected by the Squamish River discharge (May − September). Again, the effects of lower salinity (down to 7‰), lower nutrients, and increased turbidity have not been separated (Stockner et al. 1977).

Temperature — Besides the predicted Q_{10} effect on productivity and respiration (i.e. a doubling of rate for an increase of 10°C), temperature interacts with light and nutrient effects. Even though surface temperatures may range from 5 to 18°C for the strait or associated inlets, the effect of temperature changes on primary productivity and species succession has received little attention. In the winter, lower temperatures reduce the irradiance required for the onset of light saturation of photosynthesis, which is an advantage for cells already growing in a light-limited environment. However, low temperatures have been reported to be the cause of photosynthetic inhibition, which can occur on sunny days from February to April (Takahashi et al. 1973). In contrast, the elevated summer temperatures increase the nutrient demand through increased potential growth rates, a severe disadvantage in a nutrient-limited environment. Temperature has been shown to account for 17% of the variance in the assimilation number (mg C · mg chl $a^{-1} \cdot h^{-1}$) for natural populations from Saanich Inlet (Hobson 1981). Studies in Narragansett Bay have shown that there is an exponential relationship between assimilation number and temperature (Smayda 1976). In addition, because its effect on growth rate varies between species, temperature is partially responsible for the sequence of species observed in the spring−summer species succession.

Turbulence and stability — For the Strait of Georgia, uniform heating may be less important than freshwater stratification, at least in the southern part of the strait where the Fraser River plume extends over a wide area (Mackas et al. 1980). This hypothesis is supported by Parsons et al. (1981b), who observed that chlorophyll fluorescence was more closely correlated with surface temperature for stations north of Texada Island than for stations south of the island.

Frontal boundary regions of high chlorophyll fluorescence in the Strait of Georgia have been compared with calculated values of the stability expression, $\log_{10}(h \cdot u^{-3})$, where h is water depth (metres) and u is the vertically averaged water velocity (metres per second) during tidal exchange (Parsons et al. 1981b). They found low values of chlorophyll for values <0 for the term $\log_{10}(h \cdot u^{-3})$, indicating that turbulence was too great for phytoplankton growth; values >0 give high chlorophyll values due to increased stability. Areas of high chlorophyll were shown to exist at the northern and southern ends of the strait as well as among the different island groups.

For Saanich Inlet, Hobson (1981) calculated critical depth (Sverdrup 1953), and the depth of water column mixing was approximated by the stability equation ($E = (1/\rho)\,(d\rho/dz)$, where E is stability (per metre), ρ is density (kilograms per cubic metre), and z is depth (metres)) for each month for the upper 5 m. The stability of this 5-m layer was always positive. Values were usually $>30 \times 10^{-5} \cdot m^{-1}$ for the winter due to freshwater runoff and precipitation, and less during other months when heat stabilized the surface water. Ratios of critical depth to mixed depth were only <1 on one occasion due to a combination of very heavy cloud cover and turbid water, which produced a low critical depth.

Grazing — Grazing, light, and nutrients are considered to be the factors most limiting to primary production in the Strait of Georgia (Stockner et al. 1979). Grazing is discussed in detail in the section on Zooplankton.

Sinking rates — The vertical distribution of phytoplankton can be rapidly altered by the sinking of phytoplankton in the water column. At the end of a phytoplankton bloom when nitrogen becomes exhausted, sinking of large-celled diatoms, in particular, occurs. These cells are generally arrested at the pycnocline, which often coincides with the thermocline and nutricline at 5−15 m in the strait.

Stephens et al. (1967b) used sediment traps to measure the quantity of particulate matter that sedimented out of the water column in Departure Bay over a period of 1 yr. Maximum deposition of sediment occurred during the periods May−July and October−December. The first maximum occurred approximately 2 mo after the spring bloom and consisted mainly of phytoplankton cells. The second sediment maximum was derived from terrigenous material from the immediate vicinity of the coast. It was estimated that about half of the annual

TABLE 1. Recent scientific name changes of zooplankton species.

Scientific name presently in use	Name used in the past
Copepoda	
Neocalanus plumchrus	*Calanus plumchrus, Calanus tonsus*
Neocalanus cristatus	*Calanus cristatus*
Calanus marshallae	*Calanus finmarchicus, Calanus glacialis, Calanus pacificus*
Calanus pacificus	*Calanus finmarchicus*
Centropages abdominalis	*Centropages mcmurrichi*
Epilabidocera longipedata	*Epilabidocera amphitrites, Paralabidocera amphitrites*
Metridia okhotensis	*Metridia longa*
Metridia pacifica	*Metridia lucens*
Euchaeta elongata	*Euchaeta japonica, Paraeuchaeta japonica, Paraeuchaeta elongata*
Amphipoda	
Orchomene obtusa	*Orchomenella pinguis, Orchomenella obtusa*
Parathemisto pacifica	*Parathemisto japonica, Parathemisto abyssorum, Themisto abyssorum*
Chaetognatha	
Sagitta scrippsae	*Sagitta lyra*
Sagitta zetezios	*Sagitta planctonis*

primary production settled out to the sediments (see Levings et al. 1983 for further details).

No measurements of sinking rates have been made for natural populations from the strait; however, Bienfang (1981, 1982) made measurements in Saanich Inlet. Sinking rates ranged from 0.4 $m \cdot d^{-1}$ for phytoplankton assemblages dominated by small *Chaetoceros* spp. to over 1 $m \cdot d^{-1}$ when assemblages were dominated by *L. danicus* or *Thalassiosira decipiens*. Sinking rates of resting spores of *Chaetoceros* spp. were much higher than vegetative cells, the former having rates of about 2.2 $m \cdot d^{-1}$.

Sinking rates of fecal pellets produced by herbivores from Saanich Inlet, fed either diatoms or flagellates, were 123 or 88 $m \cdot d^{-1}$, respectively (Bienfang 1982). Therefore, phyletic differences in diet can influence the density of the fecal pellet and hence the vertical transfer rate of the large parcels of organic matter.

Zooplankton

The first account of British Columbia coastal zooplankton was made by McMurrich (1916) on his coastal voyage. The specimens collected and described by McMurrich 70 yr ago are typical of the late summer surface community of today. Some years later, Campbell was encouraged to complete a preliminary quantitative study of zooplankton in the Strait of Georgia (Campbell 1929a) in conjunction with Hutchinson and Lucas (1931). She described some of the more abundant copepod species (Campbell 1929a, 1929b) as well as life history stages of *Neocalanus plumchrus* and *Euchaeta elongata* (Campbell 1934). After a gap of over two decades, the description of zooplankton community structure in the Strait of Georgia by Légaré (1957) marked the beginning of sustained research interest in zooplankton.

A synopsis of the taxonomic literature of the zooplankton species in the strait was compiled by Shih et al. (1971). Since then there have been several changes and some confusion concerning the taxonomy of calanoid copepods (Table 1). For example, it has been proposed and generally accepted that the generic name *Neocalanus* be used to refer to *Calanus plumchrus* and *C. cristatus* (Bradford and Jillett 1974). In addition, *Calanus finmarchicus, C. pacificus,* and *C. glacialis* have been confused in the past. Early work (Campbell 1929b) referred to *C. finmarchicus* while later workers realized that two species were included in the classification and referred to them as *C. pacificus* and *C. glacialis* (Fulton 1968). Later, Frost (1974) described *C. marshallae* the dominant, larger congenitor, which had been referred to as *C. glacialis*. Some of the scientific name changes since 1971 are listed in Table 1. Descriptions and keys to the planktonic copepods of British Columbia can be found in Gardner and Szabo (1982).

Zooplankton Communities: Seasonal and Geographical Variations

Surface or epipelagic community — The winter community in surface waters of the strait is composed chiefly of small copepods such as *Pseudocalanus* spp., *Paracalanus parvus, Oithona helgolandica,* and *Corycaeus* sp. (Fig. 5A). *Pseudocalanus* spp. dominate this community and sustain slow growth and a low level of reproduction by grazing on small flagellates (Koeller et al. 1979). This community is most abundant in shallow water close to shore. In addition to consuming small flagellates, these copepods may utilize particulate organic material from terrestrial runoff, heterotrophic microorganisms (Seki and Kennedy 1969; Seki et al. 1969), or even microzooplankton (Takahashi and Hoskins 1978) as a food source.

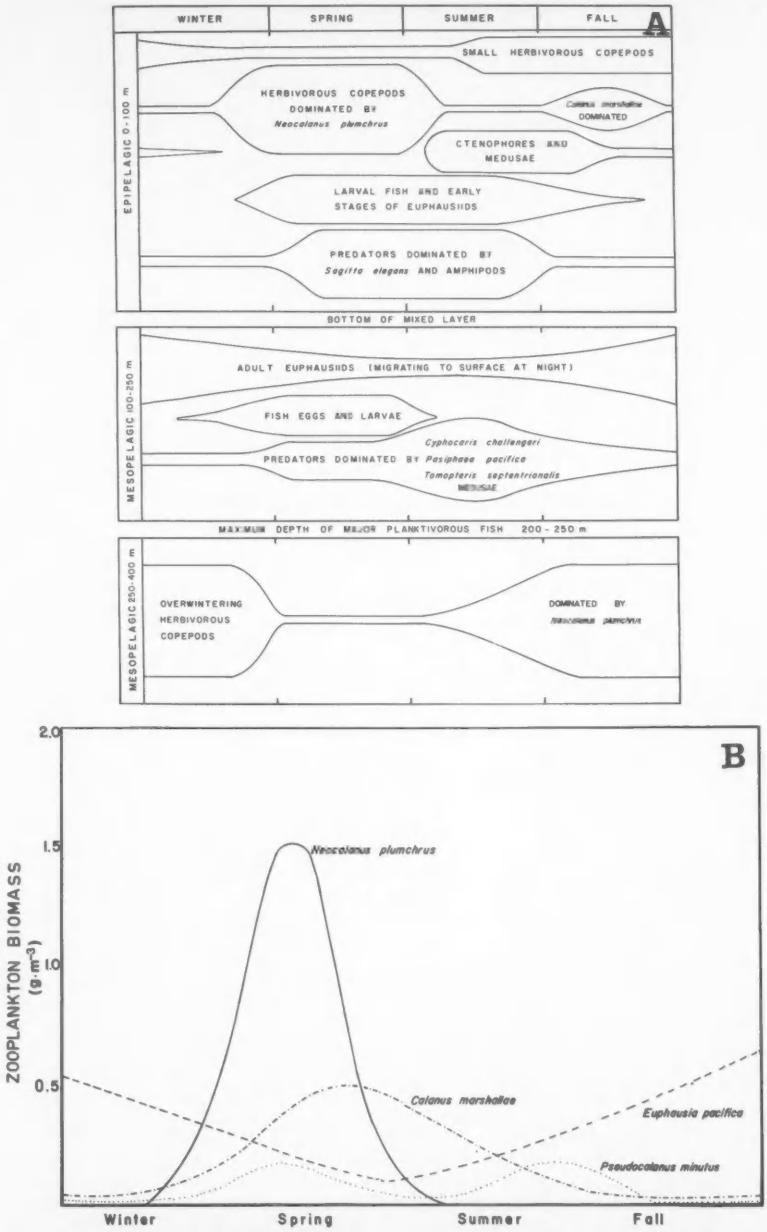

FIG. 5. Generalized schematic representation of the zooplankton community structure for the Strait of Georgia. (A) Changes in relative abundance with seasons and depth (see text for details). The biomass contours indicate major population trends and not quantitative biomass estimates. Depth ranges are approximations because many predators migrate between zones and herbivore distribution probably extends below the epipelagic zone. (B) Seasonal changes in biomass of dominant species inhabiting the upper 20–50 m of the water column. Standing stock estimates of copepods are from 20-m vertical net hauls. Euphausiid standing stock estimates are from horizontal hauls at night.

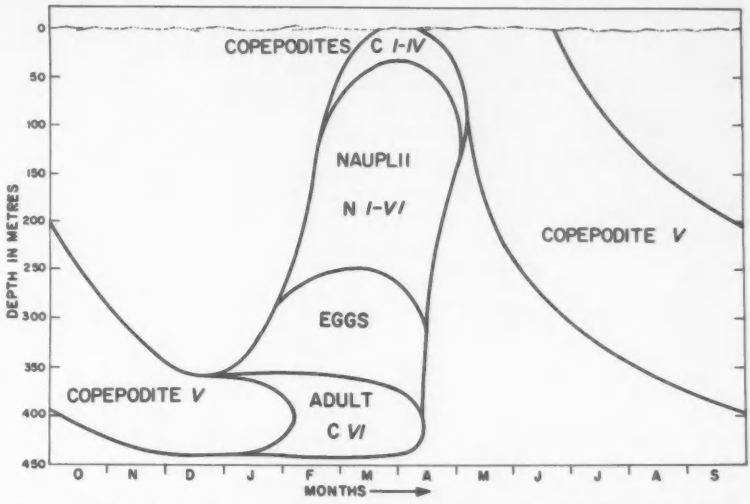

FIG. 6. Schematic representation of the life history of *Neocalanus plumchrus* (redrawn from Fulton 1973).

With the onset of the spring phytoplankton bloom the small copepod community increases reproduction. This event is overshadowed by the massive recruitment of nauplii and early copepodite stages of *N. plumchrus* from deep water to the surface (Fig. 6; Fulton 1973) and to a lesser extent by the migration of adult *C. marshallae*, *C. pacificus*, and *Metridia pacifica* from deeper water to the surface (LeBrasseur et al. 1969). *Neocalanus plumchrus* matures and breeds in the bottom water of the strait prior to and independently of the spring phytoplankton bloom. This life history strategy (Fig. 6) is considered to be a major factor contributing to the dominance of *N. plumchrus*; however, the ability to graze a wide size-range of phytoplankton may also be important (Parsons et al. 1969b). *Neocalanus plumchrus* is not as abundant in the southern portion of the strait (below the Fraser River) because this area is highly mixed and shallower (~200 m versus 400 m in the central strait) and thus less suitable for overwintering at depth. Transport from the central strait by surface currents may be responsible for the presence of small populations of *N. plumchrus* in the southern strait.

The beginning of the summer surface community is marked by the descent of *N. plumchrus* stage V into the bottom water of the strait (Fig. 5A). The concomitant decrease in grazing pressure results in increased phytoplankton production as well as accelerated growth and increased reproduction in the smaller copepods, *C. marshallae*, *C. pacificus*, and *Pseudocalanus* spp. (Stephens et al. 1969). Also, at this time there is a rapid increase in the numbers of the ctenophore *Pleurobrachia* sp. and the leptomedusa *Phialidium* sp. (Stephens et al. 1969). For the former, laboratory experiments by Greve (1977) have shown that large adult copepods can inadvertently tear the ctenophore's tentacles during regular grazing, thereby preventing rapid growth and reproduction. Greve suggests that the late summer bloom of *Pleurobrachia* may be attributed to the numerical decline of *N. plumchrus* in surface waters. In more confined waters such as Saanich Inlet, the increased predation on copepods by *Phialidium* sp. may reduce herbivore grazing pressure enough to permit a second phytoplankton bloom (Huntley and Hobson 1978).

Fall surface communities are marked by small blooms of *C. marshallae*, *C. pacificus*, *Pseudocalanus* spp., and *M. pacifica* and a decline in numbers of ctenophores and medusae (Stephens et al. 1969). Decreased solar radiation and increased depth of mixing due to storms lead to a return of winter conditions.

Saanich Inlet differs from the strait because there is no overwintering population of *N. plumchrus*, due mainly to depth differences, and the dominant copepod herbivores are *C. marshallae* and *C. pacificus* (Parsons et al. 1967). In addition, the euphausiid *Euphausia pacifica* exhibits earlier breeding and a more rapid spring growth in Saanich Inlet than in the strait where breeding and rapid growth do not occur until June when *N. plumchrus* stops feeding (Heath 1977).

Midwater community — The midwater community (from the lower boundary of the mixed layer to about 250 m; Fig. 5A) is dominated by the euphausiid *E. pacifica*, which undergoes diel vertical migration, feeding in the surface waters during darkness (Heath 1977). Adult euphausiids breed and release their eggs in surface waters during late spring, summer, and early fall; nauplii, calyptopis, and early furcilia stages of euphausiids do not migrate vertically. Heath (1977) showed that in Saanich Inlet, *E. pacifica* exhibits pulses of spawning activity, which coincides closely with periods of high phytoplankton abundance. Bary and Pieper (1970) found that the 197-kHz scattering layer of Saanich Inlet was composed of euphausiids.

The vertical movement of invertebrate predators has not

been studied in detail. Kennedy et al. (1966) found the depth range of the planktivorous glass shrimp *Pasiphaea pacifica* to lie between 30 and 250 m. It was found to feed mainly on *E. pacifica* and sometimes on copepods (O. D. Kennedy, Pacific Biological Station, Nanaimo, B.C., personnal communication). Arai and Mason (1982) reported that spring and summer population modes of the hydromedusae *Aglantha digitale* and *Aegina citrea* were below 100 m during daytime. Although *A. digitale* is known to feed on copepods, the behavior and feeding of *A. citrea* has not been studied. Arai and Fulton (1973) demonstrated diel migration of the meduse *A. digitale* by taking net hauls. In the laboratory, Reeve (1980) has examined the feeding requirements of the chaetognath *Sagitta elegans* and von Westernhagen et al. (1979) described the feeding of the amphipod *Hyperoche medusarum* on the larvae of the Pacific herrring, *Clupae harengus pallasi*.

Deepwater community — From July until the following March, the deepwater community (below 250 m) is dominated by the herbivorous copepods *N. plumchrus*, *C. marshallae*, *C. pacificus*, and *Pseudocalanus* spp. (Fig. 5A; Stephens et al. 1969). *Neocalanus plumchrus* in the preadult stage (CV) has an oil sac filled with wax esters. The sac makes up about 51% of their dry weight in June and about 39% by the following January (Lee and Nevenzel 1979). This 12% reduction in lipid reserves apparently meets the metabolic requirements of *N. plumchrus* during diapause. The remaining lipids are utilized at depth for moulting to the adult stage, breeding, and laying eggs. It is remarkable that development and reproduction can be accomplished without the adults returning to the surface and feeding as do other coastal herbivorous copepods. The deepwater community is relatively stable during fall and winter. The slight decline in numbers of overwintering copepods suggests that little predation occurs below 250 m. Many of the deepwater invertebrate predators listed by Gardner (1977) mature and become ovigerous following the breeding season of *N. plumchrus* from January through March. The peak of egg laying in March–April by important midwater fish, including Pacific hake *Merluccius productus* and walleye pollock *Theragra chalcogramma*, indicates that planktonic fish eggs and larvae could also be major food sources for deepwater invertebrate predators (J. C. Mason, Pacific Biological Station, Nanaimo, B.C., personal communication).

Nearshore community — Throughout the year, estuarine and nearshore communities are more variable than the pelagic community. This variability results from more dynamic water movements, particularly the flushing of small bays and inlets (Herlinveaux et al. 1966) and sporadic, massive recruitment of meroplankton. In these areas, copepods of the genera *Acartia*, *Pseudocalanus*, *Centropages*, and *Epilabidocera* form the more stable components of the estuarine plankton community. Decapod zoea and juveniles and barnacle nauplii form the bulk of the meroplankton (discussed in more detail by Levings et al. 1983). During extended periods of calm weather the larvacean *Oikopleura* may produce extensive blooms (Sibert et al. 1976). Zooplankton in this nearshore community are probably an important food supply for some species of salmon, as indicated by the analysis of stomach contents (Sibert and Obrebski 1976; Healey 1980).

Factors Affecting Geographic and Vertical Distribution

Physical and chemical parameters influence the distribution of marine organisms. Since temperature and salinity are two easily measured parameters, they have been used to identify and define habitats in the Strait of Georgia and associated inlets. The utility of this approach and the use of the temperature–salinity–plankton (T–S–P) diagram is discussed by Bary (1963). It is implicit in the following discussion that zooplankton samples were taken from discrete depths with opening and closing nets. Such sampling is required to identify exactly the physical and chemical properties of the environment.

Temperature and salinity — Field observations of the distribution of two planktonic ostracods in Indian Arm demonstrated that *Conchoecia elegans* occupied a greater range, including warmer water, than did *C. alata minor*. A subsequent investigation of ostracod distribution in seven British Columbia inlets showed that three inlets with bottom water warmer than 8.9°C had populations composed only of *C. elegans*, whereas the other inlets with bottom water cooler than 8.9°C contained both species (McHardy and Bary 1965).

Physical and chemical tolerances of animals can be tested in laboratory aquaria or vertical columns filled with seawater. The tolerance of euphausiids to temperature and salinity gradients were tested by placing them at the bottom of a surface-lit, vertical column of seawater and observing their vertical migration through known temperature and salinity gradients (Regan 1968). *Euphausia pacifica* from Indian Arm, where the greatest measured range of temperature and salinity existed, showed greater tolerance to changes in these parameters than *E. pacifica* taken from the open ocean; the tolerance levels of *E. pacifica* from the Strait of Georgia were intermediate. Moreover, other euphausiid species from Indian Arm such as *Thysanoessa spinifera*, *T. longipes*, and *T. raschii*, which field data indicated to be expatriate species, were less tolerant to temperature and salinity changes than the resident species, *E. pacifica*. Animals from different water masses showed an increased survival in and preference for "home" water and avoided "foreign" water of the same temperature and salinity. These observations lead to the conclusion that while temperature and salinity were important, some other "unique" properties also required explanation (Regan 1968).

Further laboratory experiments with *E. pacifica* indicated that the animals were stressed during laboratory experiments where temperature and salinity were shifted rapidly, as evidenced by a sharp decrease in respiration (Gilfillan 1970, 1972). These studies showed that stress caused by extremes of temperature and salinity were additive and that *E. pacifica*, from a stable open ocean environment, exhibited the most stress in response to extremes of these parameters. Animals from the Strait of Georgia were intermediate, while those from Indian Arm were most tolerant. However, the range of temperature and salinity that caused severe stress in the labo-

ratory experiments is only found in shallow surface waters. This would suggest that temperature and salinity affect the distribution of *E. pacifica* only in this restricted environment. It was observed that survival of experimental animals was significantly increased if they were maintained in water taken from the collection site, indicating again the importance of "undefined properties" of seawater (Gilfillan 1970).

Gardner (1977), in his analysis of the October–December community structure over a 5-yr period (1970–1975), noted some shift in dominance of the three major copepod species, *N. plumchrus*, *C. marshallae*, and *C. pacificus*, in deep water. He related population changes to a gradual increase in salinity in December at 300 m. The shift in dominance from *N. plumchrus* to *C. marshallae* was not attributed to changes in salinity per se, but rather to unspecified changes in the environment as indicated by salinity changes. This shift in species dominance is not conclusive and requires further confirmation.

Chelation of trace metals — In an attempt to understand some of the properties other than temperature and salinity that might affect marine zooplankton distributions, eggs and non-feeding nauplii stages of the copepod *E. elongata* were used for laboratory bioassays (Lewis and Ramnarine 1969; Lewis et al. 1971; Lewis 1972). Results indicated that chelation of heavy metals by naturally occurring organic compounds (complexing agents) altered the survival of test animals. Survival in the laboratory depended on a complex relationship between the nature and concentration of complexing agents as well as the concentration of trace metals (Whitfield and Lewis 1976).

Field investigations combined with laboratory studies of *E. elongata* (Evans 1973) showed that while the eggs and early nauplii may be useful stages for trace metal bioassays in the laboratory, approximately 97% of mortality in nature occurs after the egg hatches. Consequently, interaction between the egg and the environment has a minor role in determining final population size relative to other variables such as availability of food and the abundance of predators. A clear understanding of the life history stages of the species is needed to evaluate the effect of regional differences in water quality (Evans 1973).

Currents and basin flushing — In inlets and basins with sills, immigration of zooplankton species must be considered as a discontinuous process and depends, in part, on the animal moving to the appropriate water mass at the time of major water mass movement, such as the annual flushing of inlets (Krause and Lewis 1979). Exotic species may sometimes be recruited to a new environment when they are already at the limit of their geographic range but fail to survive when their water mass becomes diluted in a new location (Stone 1980). For example, in some years, *N. plumchrus* is recruited into Saanich Inlet (and likely other shallow inlets) (Stephens et al. 1967a; Fulton et al. 1969) but fails to form a resident population, probably because the overwintering population requires deeper oxygenated water than occurs in this anoxic basin.

Oxygen concentration — Investigations of vertical stratification of plankton in Saanich Inlet by Fish (1968) and Mills (1982) showed that the oxycline defined the depth distribution of *E. pacifica* and the amphipods *Cyphocaris challengeri* and *Orchomene obtusa* (stratified in that order). LD50 experiments with test animals suspended in cages in the anoxic waters indicated the three species were distributed in order of their ability to survive low oxygen levels (Fish 1968).

Hoos (1969) found that *O. obtusa* can forage in anoxic water for up to 48 h by utilizing oxygen stored in its respiratory pigments. It can replenish its supply by returning to oxygenated water.

Light — Diel vertical migration of the 12-kHz echo scattering layer in Saanich Inlet was investigated by lowering a sensitive light meter into the layer and raising it at the same rate as the evening ascent. The position of the layer was closely correlated with the 1.2×10^3 W·m^{-2} isolume (Boden and Kampa 1965). This 12-kHz echo scattering layer is thought to represent the presence of zooplankton, although it may be associated with the euphausiid layer (Bary and Pieper 1970).

Standing Stock and Production

The standing stock of zooplankton in the Strait of Georgia has generally been measured using vertical net hauls from 20, 50, or 400 m (Parsons 1979). Because of a pronounced seasonal migration by the principal copepod species, *N. plumchrus*, results from these tows are not strictly comparable and may be viewed as representing different depth zones in the strait. Thus, hauls from 20 m broadly represent the biomass of zooplankton from the euphotic zone, the zone where most of the grazing by larval fish, juvenile salmon, and herring occurs. The 50-m net hauls generally represent zooplankton found above the seasonal pycnocline, while the 400-m net hauls represent changes in zooplankton biomass over the entire water column. Estimates of biomass from various depths are summarized in Table 2 and are schematically represented in Fig. 5.

Using a 350-μm mesh net, Parsons et al. (1970) showed that the total biomass of herbivorous zooplankton reached a maximum of 1.4 g wet wt·m^{-3} (using 20-m net hauls) during May and a minimum of approximately 0.05 g wet wt·m^{-3} (using 50-m net hauls) at selected stations in the southern part of the strait during April–May. The average zooplankton biomass in 400-m net hauls shows a maximum in October–November of about 0.8 g wet wt·m^{-3} and a minimum during April–May of <0.1 g wet wt·m^{-3} (Parsons 1979). These data reflect the seasonal abundance of large zooplankton above the pycnocline in the early spring and summer and the ontogenetic migration of a large zooplankton biomass below the pycnocline during the fall and winter months.

The growth rate of zooplankton in the Strait of Georgia is difficult to assess from standing stock data because of grazing mortality and bias produced by the mesh size of plankton nets. However, two estimates of growth rate of the principal species *N. plumchrus* (Parsons et al. 1969b; Fulton 1973) showed growth rates of individuals varying between approximately 3 and 14% of their body weight per day. Fulton (1973) gives a

TABLE 2. Some approximate estimates of zooplankton standing stock and production in the Strait of Georgia and Saanich Inlet (as noted below). Production was measured over a period of approximately 3 mo during maximum growth of *Neocalanus plumchrus* and does not represent the daily production for the entire year.

Organisms	Average range of standing stock (g wet wt·m^{-3})	Production (mg C·m^{-2}·d^{-1})	Reference
Herbivorous zooplankton to 20 m	0.05–1.4	—	Parsons et al. 1970
Total zooplankton to 50 m	0.07–0.50	—	Stockner et al. 1980
Total zooplankton from selected stations to 50 m	<0.05–2.10	—	Stockner et al. 1980
Total zooplankton to 400 m	0.10–0.80	—	Stephens et al. 1969
Neocalanus plumchrus in Fraser River plume to 20 m	0.0–4.2	81	Parsons et al. 1969b
Calanus pacificus to 20 m	<0.01–0.32	—	Parsons et al. 1970
Pseudocalanus spp. to 20m	<0.01–0.03	—	Parsons et al. 1970
Euphausia pacifica	0.01–1.5	6–27	Heath (1977) (Saanich Inlet)

mean growth rate in the field of 10.6% per day from nauplius to stage V measured over a 100-d period. Parsons et al. (1969b) observed an increase in biomass of approximately 5 g wet wt·m^{-3} during the 3-mo period (March–May) which is equivalent to a production of 81 mg C·m^{-2}·d^{-1} (Table 2). This is the period of maximum zooplankton production in the Strait of Georgia. Summer, fall or winter production is generally 10% or less of the peak spring production.

Differences in zooplankton standing stock and production have been reported to occur both geographically (Parsons et al. 1969a, 1969b) and between years (Stockner et al. 1979, 1980). During April–May, Parsons et al. (1969a, 1969b) observed earlier production in the southern part of the strait for an area influenced by the Fraser River plume, compared with the northern part of the strait. Stockner et al. (1979, 1980) recorded a threefold decline in the standing stock of zooplankton from 1975 to 1976 at four stations in the southern part of the strait. Smaller scale patchiness of zooplankton populations in the Strait of Georgia has been reported by Mackas et al. (1980). This may be partially attributable to the occurrence of frontal regions in the strait; for example, Parsons et al. (1981b) found that during the summer months the greatest zooplankton biomass occurred approximately between two areas of maximum phytoplankton abundance.

Euphausiid production (*E. pacifica*) is inversely related to the production of the principal species of copepod, *N. plumchrus*. According to Heath (1977), the maximum standing stock of euphausiids occurs during the winter (October–December) with a minimum in the period March–May. The maximum standing stock of *E. pacifica* (1.5 g wet wt·m^{-3}) in the open waters of the Strait of Georgia is approximately one-fifth that found in some inlets, while the production is reported to range from approximately 6 to 27 mg C·m^{-2}·d^{-1}, or between 10–25% of that produced by copepods (Table 2). Other copepods, *C. marshallae* and *Pseudocalanus* spp., may also be very abundant in the Strait of Georgia, although due to their smaller size they do not contribute to the total biomass as much as *N. plumchrus* and *E. pacifica* (Fig. 5B). *Calanus marshallae* shows a distinct seasonal maximum late in the summer and *Pseudocalanus* spp. exhibits an increase in biomass during both the spring and fall (Parsons et al. 1970). Seasonal changes in biomass of dominant herbivorous species is summarized in Fig. 5B.

During the winter months when the standing stock of plankton in the surface waters is <0.05 g wet wt·m^{-3}, the community is composed of ciliate protozoans, metazoan nauplii, and some adult copepods of small species such as *Pseudocalanus*, *Paracalanus* spp., *Corycaeus* spp., and *Oithona* spp. (Takahashi and Hoskins 1978; Koeller et al. 1979). These animals graze mainly on nanoflagellates whose production may average around 60 mg C·m^{-2}·d^{-1} during the winter months (December–February).

The standing stock of jellyfish, ctenophores, and chaetognaths in the surface water of the strait generally reaches a maximum during the late summer months, but specific biomass estimates are not available for these groups. In Saanich Inlet, the standing stock of jellyfish and ctenophores during July was 113 g dry wt·m^{-3} or approximately 9 mg C·m^{-3} (Huntley and Hobson 1978). They found the growth rate of the principal species in this group, *Phialidium gregarium*, was about 4% body weight per day over a period of 30 d. Ctenophores (e.g. *Pleurobrachia* sp.) may be extremely

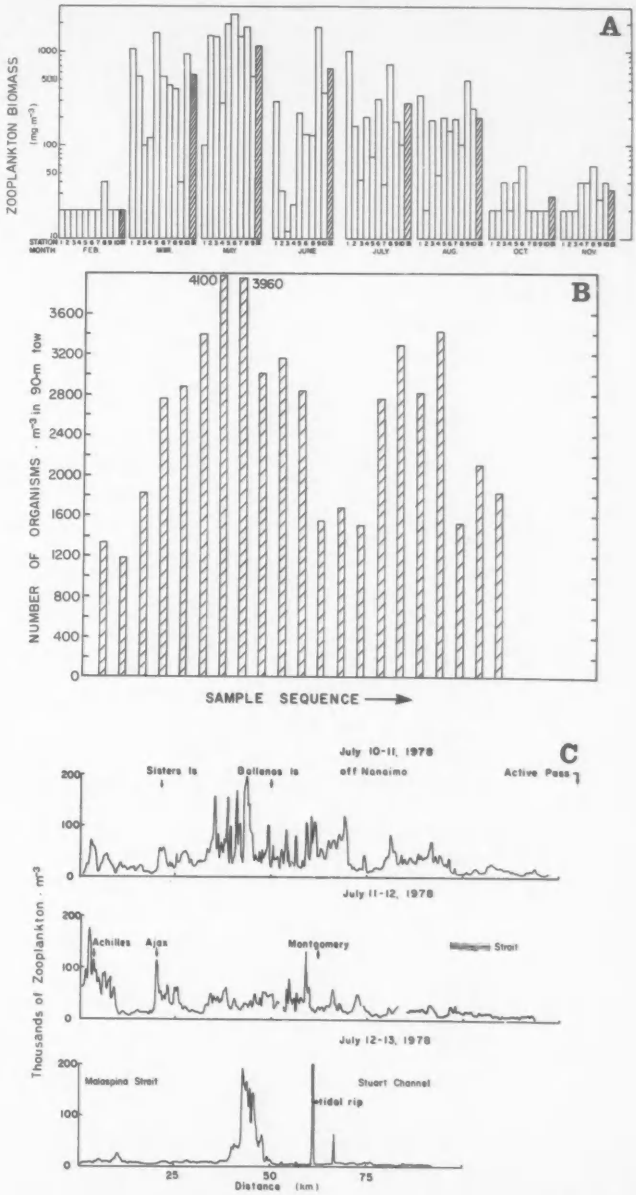

FIG. 7. Temporal and spatial variations of zooplankton biomass in the Strait of Georgia. (A) Macrozooplankton biomass wet weight (note logarithmic scale) from 20-m vertical hauls with a 350-μm mesh net. Station positions are shown in Fig. 1 (from Stephens et al. 1969). (B) Aggregation of *N. plumchrus* at the salinity front of the Fraser River plume. Longhurst–Hardy plankton recorder with 350-μm mesh, sampling horizontally in the upper 1 m at 90-m intervals (from Stephens et al. 1969). (C) Aggregation of microzooplankton (<350 μm) determined at night by using a continuous underway counter that integrated every 250–300 m at 1 m. Cruise track shown in Fig. 1 (redrawn from Mackas et al. 1980).

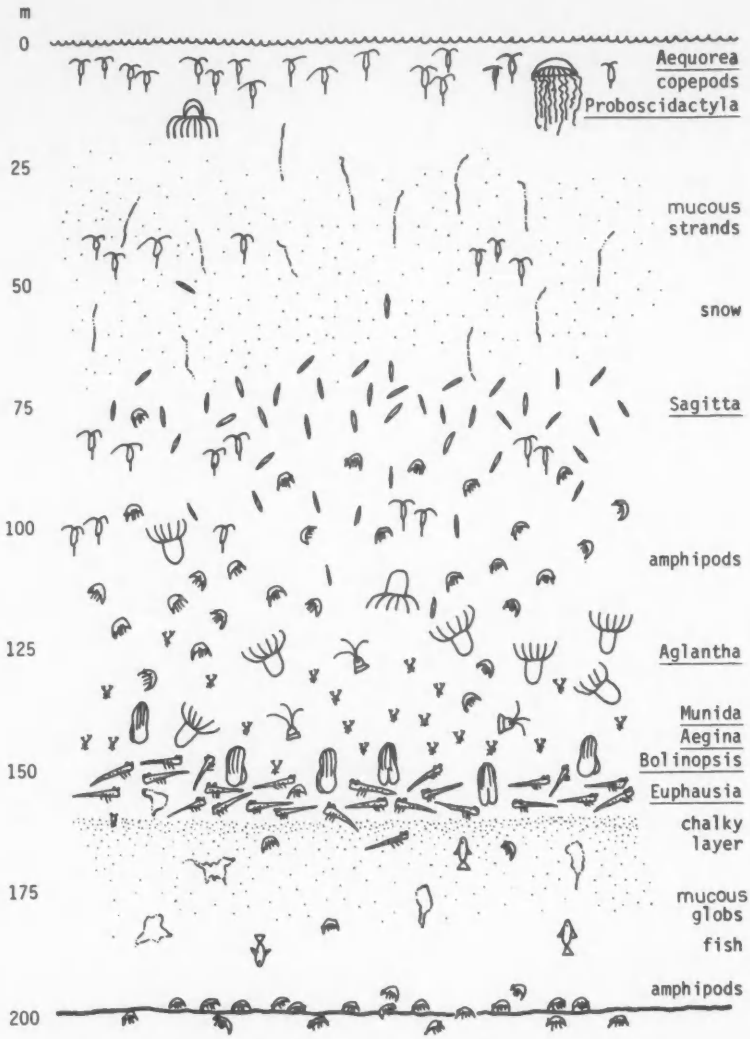

FIG. 8. A field sketch of the vertical distribution of plankton in Saanich Inlet. Observations were made during several dives using the submersible *Pisces II* (from Mills 1982).

abundant in late summer (approximately 100 individuals $\cdot m^{-3}$), while the chaetognath, *S. elegans*, has been reported in surface water from March to November; however, its seasonal and numerical abundance has yet to be fully investigated.

Recently, attention has been drawn to the potential secondary production from the remains of herring spawning in the strait (Hay and Fulton 1983). Since herring spawning is a localized phenomenon, this production is definitely important on a local scale.

Microdistribution — Experiments with planktivores in containers indicate that prey densities high enough to support growth of predators are rarely measured with traditional net hauls. LeBrasseur et al. (1969) calculated that juvenile chum salmon, *Oncorhynchus keta*, required a *N. plumchrus* concentration of $2900 \cdot m^{-3}$ or a *Microcalanus* concentration of $9300 \cdot m^{-3}$ (equivalent to a biomass of 3200 mg wet wt $\cdot m^{-3}$

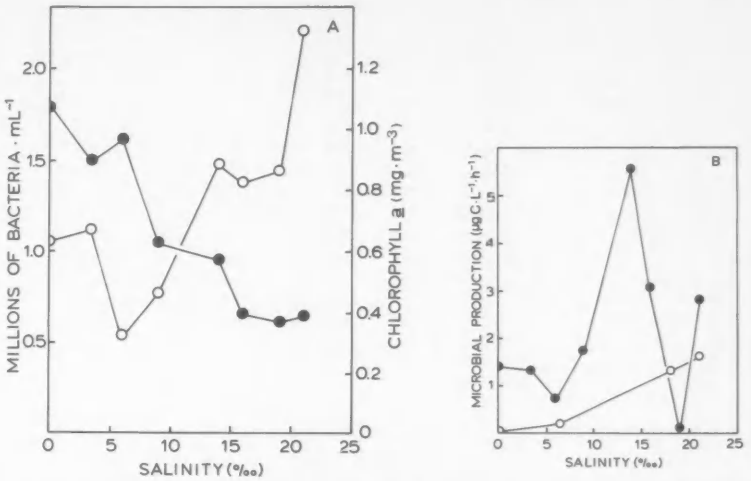

FIG. 9. Bacteria (●) and phytoplankton (○) within the Fraser River plume as a function of salinity for February 1980. (A) Standing stock; (B) production (from Albright 1983).

and 560 mg wet wt · m^{-3}, respectively) to feed to satiation. These concentrations were rarely observed in 20-m vertical hauls (Fig. 7A). However, such levels were observed in horizontally towed Longhurst–Hardy plankton recorder samples obtained from the surface waters sampled at intervals of 90 m (Fig. 7B; Stephens et al. 1969). Similarly, in culture chambers, Reeve (1980) found that *S. elegans* from Saanich Inlet fed to satiation on *Pseudocalanus* spp. concentrations of 60 000 · m^{-3}, although vertical net hauls rarely caught as many as 50 000 animals · m^{-3}. In contrast, Mackas et al. (1980) using an underway zooplankton sampling system, which takes water from 1 m and integrates counts over a horizontal distance of 250–300 m, frequently encountered patches of zooplankton with concentrations of more than 60 000 animals · m^{-3} (Fig. 7C). These examples suggest the potential importance of zooplankton patchiness in the feeding behavior of predators in a three-dimensional environment.

Physical, chemical, or biological gradients act to concentrate prey. Examples of biological aggregations caused by boundary conditions are aggregations of *N. plumchrus* at the salinity front in the Fraser River plume (Parsons et al. 1969a, 1969b; Fig. 7B), vertical migration of scattering layers (to the surface) in response to changing light levels (Bary 1967), high summer concentrations of phytoplankton (food) in areas of turbulence and consequently nutrients (Parsons et al. 1981b), and zooplankton concentrations in a tide rip (possibly a temperature gradient) (Mackas et al. 1980). Another interesting example of zooplankton aggregation is found in a study of lee waves associated with the sill in Knight Inlet (a fjord northeast of the strait), where wave trains were followed by observing the sound scattering layer with a 107-kHz echo sounder (Farmer and Smith 1980). This scattering layer, which was most dense in the least turbulent water, was interpreted as a response of plankton to a velocity gradient, although the sound scatters were not sampled (D. Farmer, Institute of Ocean Sciences, Sidney, B.C., personal communication). The foregoing examples suggest that many gradients in zooplankton biomass are found in the horizontal plane. They must be sampled horizontally and can likely be "seen" with the appropriate high-frequency echo sounder.

Recent trials by Mackie and Mills (1983) in Saanich Inlet have attempted to quantify visual observations of plankton densities from the research submersible *Pisces II*. They estimated euphausiid densities to be two orders of magnitude greater than did Bary and Pieper (1970), who used a high-speed horizontally towed plankton catcher in deep scattering layers, and more than one order of magnitude greater than did Heath (1977), who sampled horizontally in surface waters at night. Their observations indicate that other species form distinct and concentrated horizontal layers (see field sketch, Fig. 8). Such visual observations should reveal the structure of midwater plankton communities with greater resolution than conventional net tows.

In summary, the average assessment of zooplankton standing stock and production discussed in this review may represent an order of magnitude appraisal of the real situation. However, it does not represent the very high densities encountered using the fine-scale spatial resolution capabilities of a recent in situ continuous counting device (Mackas et al. 1980). Thus, for biomass budgets involving fish feeding, the standing stock estimates of zooplankton reported here may be much too low due to factors that concentrate zooplankton at some locations. The patchy distribution is probably underestimated using vertical net hauls, especially nets with a mesh greater than 350 μm, which misses most of the microzooplankton.

Few estimates have been made of nitrogen regeneration rates or the types of nitrogenous compounds released by zooplankton during regeneration. In particular, regeneration by microplankton (<200 μm) may be extremely important

because of their higher metabolic rates per unit weight compared with macrozooplankton (<350 μm).

At present, quantitative estimates of zooplankton biomass are poor except for macrozooplankton. More effort should be directed towards studies on spatial and temporal distribution of microzooplankton including life history studies. The link between zooplankton and fish is one of the most neglected areas (Parsons and LeBrasseur 1970). For example, an assessment of the importance of the density and timing of zooplankton biomass distribution in relation to larval fish survival would be a valuable starting point. Little is known about the temporal and spatial distribution of meroplankton and its importance in fish feeding and survival in shallow nearshore waters.

Bacteria

Standing Stock and Production

The distribution of bacteria in the Strait of Georgia is not well known. Recent investigations by Albright and coworkers have examined the influence of the Fraser River on bacterial distribution in the plume area (Valdés and Albright 1981; Albright 1983; Bell and Albright 1981). The freshwater bacteria are predominantly rod-shaped and larger in volume (0.13−0.5 μm^3) than their marine counterparts (0.07 μm^3) and are generally attached to particles, in contrast with the predominance of free-floating marine forms. Numbers of viable bacteria may be concentrated in the surface film (neuston) by one or two orders of magnitude, but Dietz et al. (1976) found that their heterotrophic potential was low. Bacterial numbers in surface sediments were much greater (by several orders of magnitude) than in overlying waters, and their glucose-specific activities were similar to activities in the overlying water (Chocair and Albright 1981).

The Fraser River contains 10^5 to 5×10^7 (mean 1.2×10^7) bacteria · mL river water^{-1}, which is twice as high as bacterial numbers for the strait (mean $6.4 \times 10^6 \cdot mL^{-1}$; Bell and Albright 1981; Albright 1983; Fig. 9A). Estimates of phytoplankton and bacterial carbon using chlorophyll and ATP measurements, respectively, indicated that bacterial carbon attained maximum values in the Fraser River where it accounted for up to 30−100% of the total microbial carbon. In the strait, bacterial carbon constituted only 4% (5−10 mg $C \cdot m^{-3}$) of the total carbon, the largest portion being composed of phytoplankton carbon.

Membrane diffusion chambers were used to test if Fraser River bacteria remained viable when placed in Strait of Georgia water and vice versa (Valdés and Albright 1981). Results of their experiments indicated that there may be two types of bacterioplankton populations within the freshwater of the lower Fraser River. The most numerous population (94%) is rapidly killed when the salinity of the Strait of Georgia reaches 16‰. The second, less numerous population, appears to remain viable in the strait, but it is uncertain whether this population is very active. In contrast, when the Strait of Georgia bacterial population was placed in the river water, there was little effect on the numbers of viable and total bacteria, and glucose heterotrophic activity only decreased, rather than being destroyed. Within the plume, a region where river water mixes with seawater, a stimulation of glucose heterotrophic activity (V_{max}) and bacterial production (Fig. 9B) occurred within the salinity range of approximately 3−18‰. One possible explanantion for the increased bacterial activity and productivity in the plume is the enrichment of plume water in nitrate and phosphate due to entrainment of deep water from the Strait of Georgia. Leaching of labile organic compounds from river bacteria that have recently died upon entering the higher salinity plume water may also contribute to the increase (Albright 1983). However, the latter factor is thought to be less important because the total dissolved organic concentrations were greater in the strait water than in the plume water at 1 m. River populations had a consistently lower percentage respiration than the plume or strait, possibly due to the influence of lower salinity.

Comparisons of bacterial and phytoplankton production showed that bacterial production exceeded that of the phytoplankton within river and plume waters over the salinity range of 0−17‰ in the winter (Albright 1983; Fig. 9B). In September, ratios of bacterial to photosynthetic production were 3:1 (river), 0.6:1 (plume), and 0.25:1 (strait), while in the spring at the time of the spring phytoplankton bloom the ratio was 0.04:1 in the strait (Bell and Albright 1981). These estimates demonstrate that the bacterial production during the year is relatively constant at about 3−6 mg $C \cdot m^{-3} \cdot h^{-1}$ compared with phytoplankton production. This bacterial production may be a source of food for filter feeding organisms such as nonpigmented microflagellates (Haas and Webb 1979) and microzooplankton (Seki and Kennedy 1969), especially during the winter.

Recent measurements of bacterial densities and production in Saanich Inlet indicate that they are similar to those in the strait (Fuhrman and Azam 1980). Summer population densities were about 6×10^8 cells $\cdot l^{-1}$ and production estimates ranged from 8 to 11 mg $C \cdot m^{-3} \cdot h^{-1}$, which was about 10% of the concurrent primary production. Because Furhman and Azam observed significant growth in 3 μm filtered seawater, they suggested that growth on dissolved organic carbon, or on very small particles, was more important than growth by attachment to very large particles. Taking bacterial respiration into account, Fuhrman and Azam (1980) estimated that typically 20−25% of the total carbon production passes through the bacterioplankton. Preliminary studies in enclosed water columns have shown that bacteria also play an important role in the recycling of organic nitrogen in plankton communities (Hollibaugh et al. 1980).

In analyses of potential organic carbon sources for bacterial growth, Seki et al. (1969) determined that the potential contribution of allochthanous organic matter was roughly equivalent to the primary production of the strait. What portion of this total terrestrial carbon input is usable by bacteria is unknown, but it must certainly be taken into account in food web models.

In summary, much less is known about bacteria than phytoplankton or zooplankton. Consequently, even our descriptive understanding of bacteria is poor. Studies are needed to document temporal and spatial variations on very short time scales (e.g. hours to days). The two likely roles of bacteria, food for filter feeders and recycling of nutrients, need to be carefully documented through rate measurements.

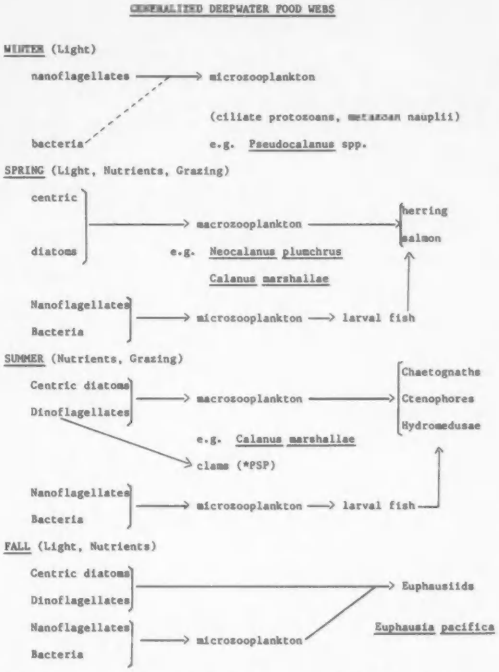

FIG. 10. Generalized schematic representation of food webs during different seasons in the Strait of Georgia. Important factors influencing primary productivity are shown in parentheses for each season. Broken lines indicate that the degree of interaction between the two trophic levels is unknown. *PSP, paralytic shellfish poisoning.

Food Webs and Models

FOOD WEBS

Pelagic — The interrelation of organisms between different trophic levels is poorly defined at present, even in more easily studied areas such as embayments and fjords (Mathews and Heimdal 1980). The best-studied interactions are between large primary producers such as diatoms and larger herbivores such as calanoid copepods and euphausiids (Fig. 10). The interaction of small primary producers (e.g. nanoflagellates) and small herbivores (e.g. ciliates, tintinnids, etc.) has rarely been examined, even though it may be very important. Increasing the complexity of the interaction, of course, is the changing size and food preference of the herbivore as it progresses through various developmental stages and also changes in the abundance of various organisms during different seasons (Fig. 10).

The role of bacteria in the food web as secondary producers appears to be important, since 20–30% of the carbon may cycle through them (Fuhrman and Azam 1980). Since their productivity is affected less by seasonal changes than phytoplankton, they may form an important alternate food source for many filter feeders during the winter (Albright 1983; Seki and Kennedy 1969).

Attempts to determine intertrophic level processes are probably best carried out in large enclosed containers or mesocosms, similar to that used by the CEPEX project in Saanich Inlet (Grice and Reeve 1982). The important advantage of these enclosures is that the same population can be sampled repeatedly, which produces a closely spaced time series of population dynamics. From this time series, important rate parameters can be determined. The numerous CEPEX studies have recently been reviewed and will not be repeated here (Grice and Reeve 1982). Generally, the organisms captured in the enclosure are the same as those in the strait and therefore, these studies are pertinent.

Attempts were made in these enclosure experiments to determine the interaction between different trophic levels by manipulating certain factors. In one experiment, a low-level nutrient enrichment (N, P, Si) resulted in increased primary production but decreased transfer efficiency from primary producers to ctenophore production (Parsons et al. 1977). In another experiment, small quantities of glucose and inorganic nutrients were added to an enclosure (Parsons et al. 1981a); heterotrophic production by bacteria depressed algal primary production, possibly because bacteria outcompeted the algae for a limited supply of nitrate. In addition, secondary and tertiary production was higher than without glucose enrichment. The last enclosure experiment attempted to compare the structure and efficiency of food chains based on diatoms and flagellates as primary producers (Grice et al. 1980).

Pelagic–benthic (paralytic shellfish poisoning) — A special pelagic–benthic food web that occurs in the strait often results in paralytic shellfish poisoning (PSP), and it is frequently referred to as "red tides" even though the two terms are not synonomous. In this web or chain, phytoplankton → shellfish → man, a toxic compound (saxitoxin) is passed along the food chain to man, often with fatal consequences. Quayle (1969) provided a review of the PSP problem in British Columbia, focusing on shellfish aspects.

On the eastern side of the Strait of Georgia, blooms of flagellates favoring more estuarine water occur. For example, the chrysomonad *Olisthodiscus luteus* (considered by some to be a chloromonad) forms yellowish brown surface blooms in water that has a salinity of less than 15‰ (e.g. Vancouver Harbour, English Bay, or near Lummi Island). In the summer of 1976 a kill of juvenile salmon at Lummi Island coincided with a bloom dominated by *O. luteus*. Also present were small numbers of diatoms and *Protogonyaulax* (*Gonyaulax*) *tamarensis*. As the samples were only from the surface, it is possible that the latter species was more abundant. *Olisthodiscus luteus* has not been shown to produce extractable toxins in culture (R. Andersen, Department of Oceanography, University of British Columbia, Vancouver, B.C., and R. A. Catolico, Department of Botany, University of Washington, Seattle, WA, personal communication). White (1980) has found that *P. tamarensis* is toxic in oral dose to fish, including young salmon. Its impact on fish resources in British Columbia water has not been investigated yet.

Paralytic shellfish poison (PSP) has been linked to three dinoflagellate species in this region: *Protogonyaulax* (formerly *Gonyaulax*) *catenella* (Taylor 1968; Quayle 1969; Norris

and Chew 1975), *P. acatenella* (Prakash and Taylor 1966), and *P. tamarensis* (Taylor 1975). Human fatalities have occurred at Theodosia Inlet in the northern Strait of Georgia (1965, described by Prakash and Taylor 1966) and at Gilford Island immediately to the north of the strait (1980, causative organism unknown). Other fatalities have occurred outside the region (see Quayle 1969 for details).

It is not certain if all PSP in these waters is due to this *Protogonyaulax* spp. complex. On several occasions blooms of the dinoflagellates *Prorocentrum micans* and *Cochlodinium citron* have been found in the vicinity of shellfish with elevated toxic levels, but neither has produced saxitoxin-like compounds in pure culture (F. J. R. Taylor and R. Waters, Department of Oceanography, University of British Columbia, Vancouver, B.C., unpublished observations).

Phytoplankton blooms, frequently dominated by a dinoflagellate, often discolor the water, yielding a reddish hue. This phenomenon is referred to as a red tide; however, in the case of nondinoflagellate blooms, use of the term "red water" is preferred. Quayle (1969) provided a few records of red water blooms, noting that two of the most common causes of nontoxic blooms are the dinoflagellates *Gymnodinium sanguineum* (= *splendens*) and *Noctiluca scintillans*. This is true mainly for the western Strait of Georgia and Juan de Fuca Strait. *Gymnodinium sanguineum* has produced intense blooms in protected bays at several Vancouver Island localities, such as Ladysmith Harbour (Quayle 1969) and Esquimalt Lagoon (Watanabe and Robinson 1979). It is usually harmless, although Nightingale (1936) reported oyster kills, apparently resulting from a bloom of this species, in Oakland Bay and Skookum Inlet, Washington. *Noctiluca* is particularly common at convergence zones near the southern Gulf Islands where it accumulates due to its buoyancy, but it is also common in summer in sheltered bays throughout the region down to southern Puget Sound. Because it is phagotrophic, *Noctiluca* must follow blooms of its food organisms, usually diatoms, but the cells are almost invariably empty when they are concentrated at the surface, possibly after the food has been depleted.

Another very common source of red water is the ciliate, *Mesodinium rubrum* (Taylor et al. 1971), which causes diffuse maroon discolorations over wide areas of the southern Strait of Georgia and Juan de Fuca Strait. It is unusual in that it usually blooms in early spring or late fall, even into winter. Because much of this information on British Columbia red water is unpublished, a more complete description will be published later (F. J. R. Taylor, unpublished data).

In view of the serious consequences of red tides to British Columbia shellfish exploitation, it is remarkable how little research has been done on this problem. Greater provincial and federal government interest seems called for, particularly because the patchy and sporadic nature of toxic blooms make adequate sampling logistically difficult.

MODELS

There have been no comprehensive models developed to describe and predict the dynamic aspects of phytoplankton and zooplankton production in the strait. To date, most models have been simplistic and they have used only one or two biological processes to predict changes in standing stock.

Employment of Sverdrup's (1953) critical depth model has been used to demonstrate that only from March to October are conditions stable enough to allow primary production to proceed unrestricted by the amount of light in the mixed layer (Parsons 1979). This approach has been expanded upon by Takahashi et al. (1973) in their simulation model of the Fraser River Estuary. They developed a physiologically based model to describe phytoplankton distribution in which variations in maximum photosynthetic rate as a function of light intensity were attributed to environmental factors such as nutrient concentration and temperature. Their model showed that light was limiting the photosynthetic rate in surface water in December and January. The interaction of other factors such as temperature and nutrients with photosynthesis and light resulted in photosynthetic inhibition from February to April at the surface and in nutrient restricted photosynthesis from July to August. While this relatively successful model was one of the first to employ the factor interaction approach in predicting photosynthetic rate, the authors felt that its principal inadequacy was its inability to predict changes in the structure of the phytoplankton community. These changes are known to be important to size-selective grazing of herbivorous zooplankton (Parsons et al. 1967).

Development of more complex short-term models to describe the dynamics of phytoplankton blooms in Puget Sound (Winter et al. 1975) and the northeast Pacific Ocean (Jamart et al. 1977) have been relatively successful. Fortunately, in the Puget Sound investigation, field measurements were carried out with sufficient frequency to allow investigation of physical and biological processes with time scales on the order of a day. In this numerical model the hydrodynamic conditions were represented by an approximate analysis of the gravitational convection mode of circulation. Changes in phytoplankton standing stock were represented by changes in photosynthesis and respiration, sinking rates, herbivore grazing, and mixing and advection in the water column. The model was able to reproduce principal features of variations in phytoplankton biomass over periods of 35–75 d.

The use of enclosures to contain a portion of the water column for an extended period of time allows the modeler to simplify the physical aspects of a model (e.g. eliminate horizontal advection) and increase the biological detail through the use of a number of submodels. This approach was used by Carruthers (1981) and Sonntag and Greve (1977) for modeling some experiments conducted in experimental enclosures in Saanich Inlet. Carruthers (1981) attempted to model changes in phytoplankton and bacterial standing stocks over a 75-d period during which nutrients were added weekly to an enclosure that was mixed continuously in the upper one-third of the water column. The model was physiologically based, with photosynthetic rate being modified by light, nutrients, and temperature and phytoplankton density being governed by grazing, sinking, and mixing. The principal species of the phytoplankton community were divided into four functional groups, large and small cells of diatoms and flagellates. The model was relatively successful in simulating the development of the phytoplankton bloom, but it was completely inadequate in simulating the sudden crash of the diatom bloom that occurred in the enclosure. The explanation for the

model failure was that physiological parameters, which are considered to be constant in the model, must vary markedly during the onset of the crash period.

In summary, much of the past research has concentrated on determining geographic and seasonal differences in phytoplankton standing stock (chlorophyll *a*) and primary production ($^{14}CO_2$ uptake). Zooplankton measurements have generally been limited to wet weight estimates of the standing stock of large species (>350 μm) and a general description of their life cycles. The assessment of food web dynamics from these limited standing stock measurements is often inaccurate and frequently misleading because of the absence of data on how rate processes affect standing stocks. The processes oriented approach has been used successfully in other areas such as the Peruvian upwelling (Walsh et al. 1978) and the Nova Scotia shelf (Fournier et al. 1977) and this approach should be adopted for future studies in the Strait of Georgia. This would involve assembling a scientific team consisting of a physical oceanographer, a mathematical modeler, and a bacterial, a phytoplankton, and a zooplankton physiologist/ecologist. State-of-the-art equipment (continuous underway sampling for nutrients, fluorescence, temperature, and zooplankton and aircraft and satellites with fluorescence detectors) should be used to assess spatial and temporal patchiness. More closely spaced time series are needed, especially for spring and summer phytoplankton blooms (Harris 1980). Assessing the rates of these biological processes in the field is often difficult because the same population cannot be revisited. The use of small experimental enclosures should be used to complement direct field measurements of bacteria–phytoplankton–zooplankton interactions. Enclosures would also be useful for investigating the importance of the coupling of pelagic–benthic processes.

Retrospects and Prospects

It is evident from our review that major research efforts have been directed towards understanding the dynamics of the larger phytoplankton and zooplankton components of the pelagic ecosystem, "mapping" the temporal and spatial distribution of planktonic biomass, and studying some physical and chemical factors affecting distributions of plankton. None of the work reviewed was specifically designed to solve fisheries problems. The lack of joint projects between fisheries scientists and oceanographers has sometimes been attributed to philosophical differences in approaches to science (see for example Parsons 1975; Rigler 1982). However, the more pragmatic problem of different time scales and levels of funding for experimental work (Fig. 11) may be a greater deterrent to successful collaboration. For example, a microbiological experiment taking days and costing a few hundred dollars is not likely to be performed in conjuction with a fisheries experiment taking several years and costing several hundreds of thousands of dollars, unless there is a clear understanding of the difference in scales between participating researchers, and dedicated intellectual and logistic support for the duration of such a project.

Fisheries science in Canada is undergoing a transition from management of single fish stocks to the management of the entire fish component of an ecosystem (e.g. Mercer 1982).

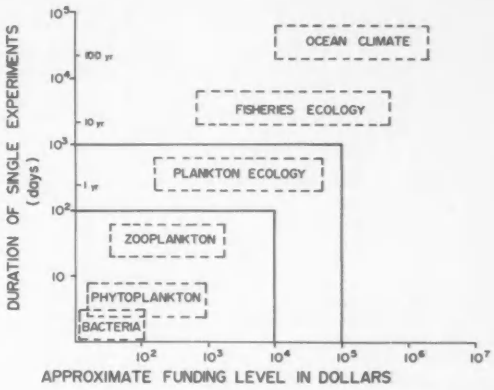

FIG. 11. Time scales and monetary requirements for experiments conducted on different parts of the food web.

Implicit in this strategy is a need to understand the biotic and abiotic environments of fishes and also the necessity for a shift in emphasis from research by disciplines or on single species of fish to interdisciplinary research on ecosystems. While there are many critical small-scale experiments required to improve our current understanding of parts of the Strait of Georgia food web, e.g. nitrogen budgets, the role of dissolved and particulate organic matter, the role of microorganisms, etc., larger scale experiments that are more relevant to the understanding of fisheries ecosystems lie in the scale that we have designated in Fig. 11 as "plankton ecology." The following experiments seem particularly amenable to a multidisciplinary approach.

The early life history of the Pacific herring (*Clupea harengus pallasi*) requires a study of the physical and chemical environment of the spawning grounds, an analysis of its food web, and an estimate of sources of mortality during the first few months after hatching. In our estimation, such a study could be carried out in a small enclosed basin such as Hidden Basin (Fig. 1).

The study of interactions during the early larval stages of the midwater spawning species Pacific hake (*Merluccius productus*) and pollock (*Theragra chalcogrammus*) is another example where a multidisciplinary approach would be beneficial, although the logistics of a suitable field program would require a greater deal of planning and coordination.

Physical, chemical, and biological gradients that lead to the formation of biological fronts are presently being studied at the lower end of the food web. In our view the study of the feeding ecology and interaction of juvenile and adult fish in such microenvironments would be greatly enhanced, especially if existing programs could be expanded to include vertical as well as horizontal boundaries.

The verification of fisheries models from field observations will always be costly. However, we expect that well-coordinated multidisciplinary studies on critical sites will most likely lead to significant new insights into the interaction between biological oceanography and fisheries.

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History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia[1]

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KETCHEN, K. S., N. BOURNE, AND T. H. BUTLER. 1983. History and present status of fisheries for marine fishes and invertebrates in the Strait of Georgia, British Columbia. Can. J. Fish. Aquat. Sci. 40: 1095–1119.

An historical account is given of the development of Strait of Georgia commercial fisheries (other than salmon) from their beginnings in the middle to late 19th century to the 1980s. Where possible, attempts were made to explain past fluctuation in abundance, especially to distinguish natural effects from those of fishing or socioeconomic origin. The review deals with commercial exploitation of herring (*Clupea harengus pallasi*), dogfish (*Squalus acanthias*), lingcod (*Ophiodon elongatus*), Pacific cod (*Gadus macrocephalus*), English sole (*Parophrys vetulus*), pollock (*Theragra chalcogramma*), hake (*Merluccius productus*), Dungeness crab (*Cancer magister*), shrimps (*Pandalopsis dispar, Pandalus platyceros, P. jordani, P. hypsinotus* and *P. danae*), oyster (*Crassostrea gigas*), butter clams (*Saxidomus giganteus*), little neck clams (*Protothaca staminea*), Manila clams (*Tapes phillipinarum*), geoduck clams (*Panope generosa*), and other invertebrates. Lingcod and the various shellfish species are also the object of recreational fisheries. Commercial landings in 1980 totalled 25 575 t with a landed value of over 20 million dollars. Over 57% of the weight landed and 70% of its landed value consisted of herring. Oysters, geoduck clams, Pacific cod, and Dungeness crabs were next in importance. We conclude that the future of the fishery will depend on policy regarding the coexistence of commercial and recreational components, the effectiveness of management measures, and probably on the success of controlling domestic and industrial pollution.

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Ce qui suit est un historique du développement des pêches commerciales (autres que celles des saumons) dans le détroit de Géorgie depuis les débuts, du milieu à la fin du 19e siècle, jusqu'à nos jours. Autant que possible, on explique les fluctuations d'abondance passées et surtout on s'efforce de séparer les effets naturels de ceux qui résultent de la pêche ou de facteurs socio-économiques. On y traite de l'exploitation commerciale des espèces suivantes: hareng (*Clupea harengus pallasi*), aiguillat (*Squalus acanthias*), ophiodon (*Ophiodon elongatus*), morue du Pacifique (*Gadus macrocephalus*), sole anglaise (*Parophrys vetulus*), morue du Pacifique occidental (*Theragra chalcogramma*), merlu du Pacifique (*Merluccius productus*), dormeur du Pacifique (*Cancer magister*), crevettes (*Pandalopsis dispar, Pandalus platyceros, P. jordani, P. hypsinotus* et *P. danae*), huître (*Crassostea gigas*), palourde jaune (*Saxidomus giganetus*), quahaug du Pacifique (*Prothothaca staminea*), palourde de Manille (*Tapes phillipinarum*), glycimère (*Panope generosa*) et autres invertébrés. L'ophiodon et les diverses espèces de crustacés et mollusques sont également l'objet de pêches récréatives. Le total des débarquements commerciaux en 1980 était de 25 575 t, d'une valeur au débarquement de plus de 20 millions de dollars. Le hareng représentait plus de 57 % du poids et 70 % de la valeur débarquée. Viennent ensuite les huîtres, les glycimères, la morue du Pacifique et les dormeurs du Pacifique. Nous concluons que l'avenir de la pêche dépendra d'une politique de co-existence des composantes commerciale et récréative, de l'efficacité des mesures de gestion et probablement du succès à contrôler la pollution domestique et industrielle.

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In preparing what appears to be the first general account of fisheries of the Strait of Georgia, we have endeavored to provide an historical perspective to highlight long-term trends in production and, in cases where effort information is available, to note apparent trends in abundance. For the special benefit of present and future fishery biologists and oceanographers our task will be to comment on the causes of these trends and to point out instances where natural oceanographic events appear to have played a significant role in shaping the courses of fisheries, as opposed to man-made events such as the effects of fishing, changes in regulatory measures, effects of pollution, and a variety of socioeconomic circumstances.

Within the time constraints of the symposium on fisheries and oceanography at which this paper was presented, it was found necessary to exclude a review of fisheries for anadromous species. This is a major shortcoming in view of the overwhelming economic and recreational importance of the salmon fisheries. However, the exclusion is not without some logic since all five species, if not all stocks of each species, spend most of their life in offshore waters and in varying degrees use the Strait primarily as a pathway to and from their rivers of origin. Furthermore, and again in varying degrees, these stocks are fished both inside and outside the Strait of Georgia when mixed with stocks from still other areas of the coast. Thus, except perhaps for the sockeye salmon (*Oncorhynchus nerka*) of the Fraser River, statistics–abundance data present serious problems of interpretation that are best left for other specialists to solve. If further justification be needed, we would point to the fact that relatively little is known about the role of the marine envionment in general, and the Strait of Georgia in particular, in determining the size of an adult salmon run and that (to date at least) there is nothing to suggest that variations in route of migration of these adults into the Strait of Georgia are determined by events within the Strait itself.

We set our sights then on a review that deals only with marine fishes and invertebrates — species that are more or less full-time residents of the Strait or at least spend the most crucial period of their life history in that body of water.

Materials and Methods

In reviewing fisheries of long standing, we have adopted a simple format that consists of (i) a capsule sketch of the life history of the species concerned, (ii) definition of stocks, (iii) consideration of trends in production, and (iv) a forecast of the future prospects for each fishery. Some fisheries are new (3–6 yr old) and some are defunct, and these will be dealt with in a different manner.

Statistical Sources

For accounts of the early beginnings of fisheries, if not already published by other authors, reliance has been placed on annual reports of the Department of Marine and Fisheries. From the 1870s to 1904 they dealt with British Columbia as a whole but from 1905 to 1917 presented a verbal and statistical record by three districts. Two are germane to the present study: district 1 represented Vancouver and vicinity, and except for certain species, accounted for landings from the Strait of Georgia; district 3 represented both the east and west coasts of Vancouver Island and adjacent mainland not included in the Vancouver district. For district 3, catches were reported by coastal areas, thus permitting a distinction of production in east coast areas, which when combined with that of district 1 provided an approximate record of production from the Strait of Georgia as a whole. This system of recording was maintained from 1917 to 1946 in publications of the Dominion Bureau of Statistics. From early days until 1938–40 (depending on the species considered) production records are presumed to be relatively reliable, but by the beginning of World War II, many fisheries that previously had been localized were joined by vessels that were capable of fishing on grounds both inside and outside the Strait of Georgia during the course of a single trip. Also, there was increased centralization of landings at Vancouver. Thus, in a short period of years, port-of-landing records ceased to be even roughly indicative of area of catch.

This deficiency was soon recognized by the Canadian Department of Fisheries (Pacific Region) and the statistical system was redesigned with the view to obtaining better information on area of catch. A "sales slip" system was introduced in 1951 and statistics were thenceforth published directly by the Department.

In some cases the ca. 1938–50 hiatus of information on production in the Strait of Georgia was bridged in part by distribution of logbooks by the Fisheries Research Boad of Canada (FRB) and/or maintenance of FRB representatives at important ports of landing. For the otter-trawl fishery this had its beginning in 1945–46, whereas detailed records on the herring fishery were collected as early as 1933–34 (Tester 1935). For other fisheries, however, it was not until 1951 that more reliable records of catch by area were published. Thus, in this report the reader will see frequent reference to the gap between 1938–50 and the dependence on records since 1951 to indicate production and abundance trends.

Since it is now impossible to verify the accuracy of early records from the early 1900s to the late 1930s, they must be treated with caution and be regarded only as approximations of historical events.

The system adopted in 1951 has been reasonably satisfactory for fisheries not involving highly mobile operations, and fishing effort information ("days fishing") has been generally useful especially for fisheries characterized by day-boat or short-trip operations, but such records are not sufficiently refined for detailed analysis.

Records of catch and effort in the groundfish fishery have been complemented by data collected by interview and logbook records and have been published annually since 1966 in the general format used by Smith (1981).

Definition of Study Area

For present purposes the Canadian portion of the Strait of Georgia is defined by Department of Fisheries and Oceans statistical areas 13–19 inclusive and areas 28 and 29 (Fig. 1). In some cases, e.g. for the trawl fishery, statistical areas 12 (Queen Charlotte Strait) and 20 (Juan de Fuca Strait) are included as part of an international system in which the Canadian portion of the Strait, Queen Charlotte Strait, and Juan de Fuca Strait are combined as area 4B, while the United

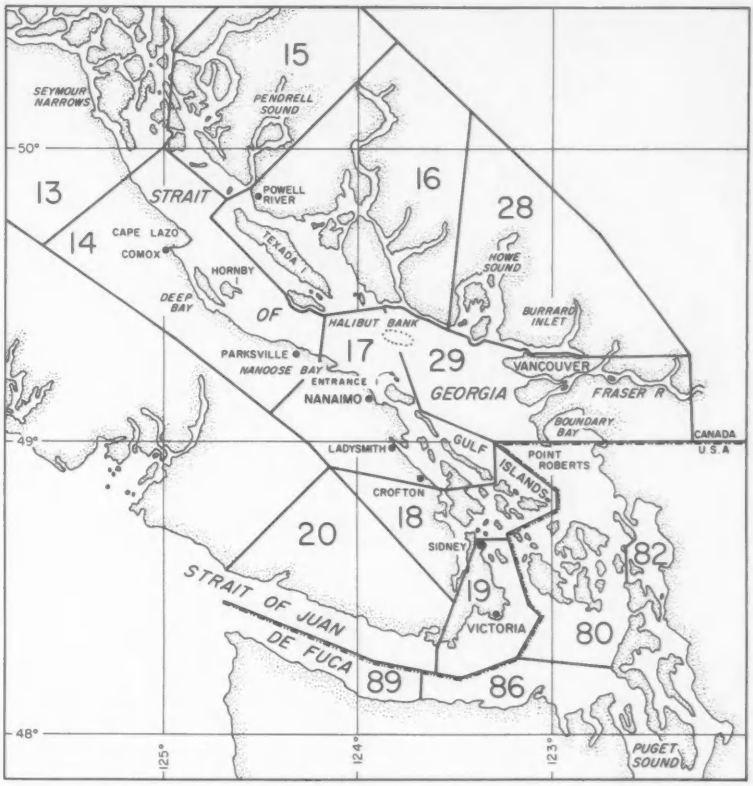

FIG. 1. Strait of Georgia and adjoining Juan de Fuca Strait and Puget Sound showing minor statistical areas employed by Canada and the United States.

States portion of the Strait, Puget Sound, and Juan de Fuca Strait are denoted as area 4A. Within this latter area there are minor statistical areas similar to those in British Columbia, with minor area 80 being recognized as the Strait of Georgia. These minor area statistics are not available for all species and all years in which case, and where necessary, records applying to the larger area 4A will be used.

In the case of historical herring statistics, the Strait of Georgia is identified as the middle east coast (MEC) and lower east coast (LEC) of Vancouver Island and the Vancouver District. These are represented by minor statistical areas 13–17A, 17B–19, and 28–29, respectively.

These area discrepancies among fisheries and nations are of minor importance in the present analysis. In few cases does the inclusion or exclusion of individual minor areas alter the general synopsis.

Summarizing, the reader should recognize that the historical records possess some breaks and are probably not of uniform accuracy and that the geographical definition of the Strait of Georgia is subject to some flexibility depending on the species being considered.

Fisheries of the Strait

Most of the Strait of Georgia fisheries occur on or over depths less than 90–100 m and are thus confined to a relatively narrow band around the periphery of the Strait. Within that band most of the production of herring, cod, flounders, shrimps, and clams (to be discussed in more detail below) comes from waters along the east coast of Vancouver Island from Cape Lazo to Sidney (Fig. 1) where the bottom is relatively smooth, consisting of sand and/or mud. Exceptions are the area 13 part of Vancouver Island and the portion of area 17 between the north end of the Gulf Islands and Parksville where rock or reef dwelling species (lingcod, prawns, dogfish) predominate.

On the mainland side of the Strait, soft or smooth bottom is confined mainly to waters near Vancouver (areas 28–29) southward into the United States sections of the Strait (area 80). The remainder of the mainland coast (areas 15 and 16) consists of hard rocky bottom and is relatively unproductive except for lingcod, prawns, and dogfish.

Not until the late 1970s did fisheries begin to develop in

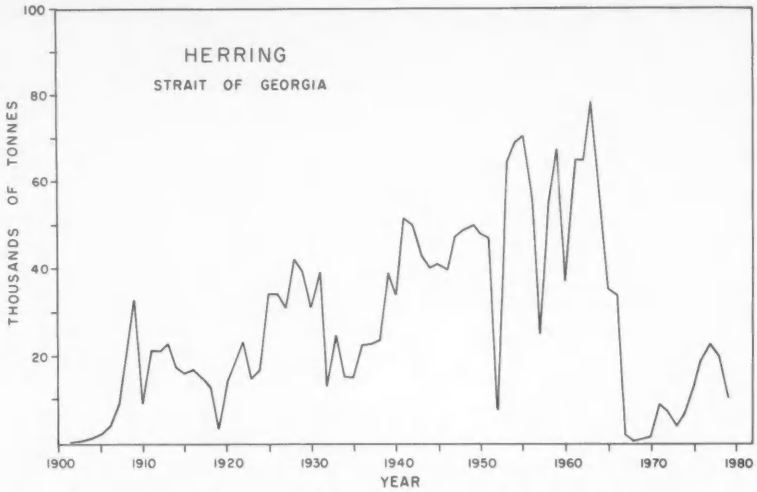

FIG. 2. Historical production of herring by the Canadian fishery in the Strait of Georgia using a combination of the traditional middle and lower east coast areas (equivalent to minor statistical areas 13–19 and 29). (Data from Taylor 1964; Hourston 1980, 1981).

waters overlying the deep (100–400 m) central portion of the Strait, but then only for two pelagic fishes (pollock and hake). A fishery for crustaceans occurs on rocky shoals like Halibut Bank, surrounded by deep water, but otherwise the deep part of the Strait is relatively unproductive of marketable bottom-dwelling animals.

HERRING (*CLUPEA HARENGUS PALLASII*)

Life cycle — Herring lay their adhesive eggs on fixed vegation (eelgrass and various species of rockweed algae) in or immediately below the intertidal zone (Taylor 1964; Hourston and Haegele 1980). Spawning in the Strait of Georgia takes place during March and incubation takes about 2 wk. During the first few days of the larval stage lasting 10 wk the young are at the mercy of tidal and wind-driven currents. As swimming ability improves and the larvae metamorphose into a recognizable adult form (June–July) they congregate in increasingly larger schools. With the approach of autumn, the schools move gradually seaward to wintering grounds on the continental shelf: off the lower west coast of Vancouver Island and northern Washington for those departing the Strait from the south; in Queen Charlotte Sound for those exiting to the north.

With the onset of maturity, usually at age 3–4 yr, herring migrate from the open waters to the Strait in autumn months and return following spawning in March. This process continues for the remaining few years of the herring's life span.

Stocks — Results of tagging conducted in the 1940s and 1950s suggest the presence of nine major migratory populations in Canadian waters, of which two are identified with the Strait of Georgia (Taylor 1964). These were formerly designated as the LEC and MEC populations. Although they were relatively discrete there is some mixing, about 25% of tagged fish in the 1st yr being observed to emigrate into adjacent populations. According to Stevenson (1955) the MEC population receives its largest proportion of immigrants from the LEC population. Emigrants from MEC are primarily to LEC, while emigrants from the LEC population are in relatively low and equal proportions to the MEC and lower west coast (LWC) of Vancouver Island population.

The relationship of juvenile to adult populations of herring is not clearly understood. The former appear to engage in a substantially greater amount of wandering (Taylor 1964), and perhaps this can be expected in view of the limited area provided by a narrow continental shelf for distribution of juveniles of several populations off the southwest coast of Vancouver Island.

For review purposes we have presumed that the LEC and MEC populations can be treated as a unit even though they were formerly managed separately and currently by even smaller sections.

We have also presumed that herring entering United States waters of the Strait and Puget Sound belong to a stock that is largely separate from that occupying the Canadian portion of the Strait. Some exchange has been indicated in results of recent tagging, e.g. a few recaptures at the site of the United States roe fishery in area 80 from tagging conducted in the Gulf Islands portion of Canadian areas 17 and 18, and a few in the latter areas from tagging in United States area 80 (Haegele et al. 1982; C. W. Haegele, personal communication).

History of the fishery — Aboriginal utilization of herring dates from at least as early as 800 B.C., while first commercial

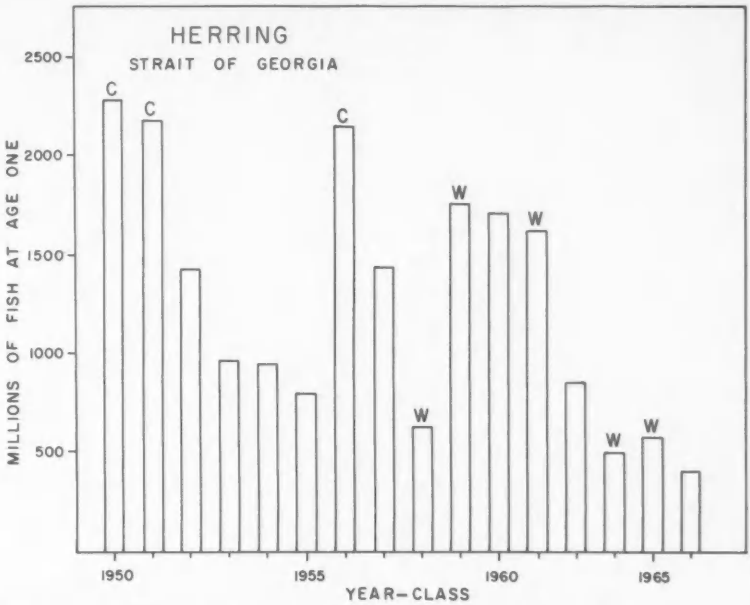

FIG. 3. Estimates of Strait of Georgia herring year-class strengths (from Hourston 1980) compared with average surface temperature for the (spawning) month of March (from Hollister and Sandnes 1972). *C* and *W* indicate temperatures at least 1°F below or above the long-term mean (44.9°F), respectively.

production was reported in 1877 (Hourston and Haegele 1980). From then until the beginning of the present century, landings ranged from 130 to 650 t, all from the Strait of Georgia and mostly with the use of drag or beach seines. Drift gill-nets were in wide use by 1905, followed by purse seines in about 1910 (Tester 1935).

By 1904 and from then until 1934, most of the catch was exported in a dry-salted form to markets in the Orient. Production from the Strait of Georgia reached a peak of 42 000 t, after which unsettled market conditions reduced production to only 13 000 t in 1932 (Fig. 2).

The years 1935–67 marked the era of the reduction (meal and oil) fishery which took place in the late fall and winter months and involved purse seines almost entirely. From near the beinning, catch quotas were introduced, but with frequent granting of extensions these limits had little effect on production. As markets expanded, production from the Strait of Georgia, interrupted in several years by industrial strikes (e.g. fishing years of 1952–53 and 1957–58), rose to more than 70 000 t by the mid-1950s and an all-time high of 78 000 t in the 1963–64 season.

In the Strait of Georgia, herring abundance appeared to be highest in the 1949–50 to 1953–54 seasons but was still high during the 1959–60 to 1963–64 period (Hourston 1980). Then catastrophe struck. There appeared to be a sudden drop in abundance following or simultaneous with a sharp increase in the rate of removal. The spawning escapement of 1965 fell to half that in 1964 and to only 10% in the succeeding three spawning seasons (1966–68) (Hourston and Nash 1972). Yet, catches remained relatively high, decreasing by an average of less than 10% in the 1963–64 to 1966–67 fisheries from the average during the 1958–59 to 1962–63 period.

In 1967–68, the Strait of Georgia was closed to all but a small operation for bait and food herring. Hourston (1980) attributes the failure to recognize the collapse of the Strait of Georgia stocks (as well as all others along the coast) to several factors: (1) recruitment of several successive weak year-classes (1963–65), (2) greatly increased efficiency of the seine fleet, and (3) underestimation of the declining size of spawning escapements during the 1960s.

The weakness of herring year-classes immediately prior to collapse of the fishery is illustrated in Fig. 3. It also provides an indication that at least some weak year-classes were produced in years when sea surface temperatures of the Strait during the spawning month (March) were relatively high. On the other hand, strongest year-classes occurred when temperatures were relatively low. Expectedly, the statistical relationship is not strong ($r = -0.55$, significant at $P = 0.05$), but it suggests that water temperature or some related factor(s) at time of spawning has a bearing on success of egg to larval survival (K. S. Ketchen, unpublished data). To say more without closer study by herring investigators would be inappropriate. When the fishery on recovered stocks reopened in 1971 it had assumed a new character. This is the roe herring era that takes place in March immediately before spawning. The current magnitude of removals as shown in Fig. 2 (roe

as well as bait and food herring) is not indicative of current stock size. Actually, recovery was much better in the Strait than elsewhere (R. D. Humphreys, Fisheries Management, Vancouver, personal communication). Fishery managers, faced with difficulties of effort control and predication of abundance plus heavy political pressure from sport fishing interests, have seen fit to place severe restrictions on commercial operations in the Strait.

Historically, the Washington herring fishery has been a minor one compared with that in Canadian waters, rarely exceeding 500 t prior to 1957. It began in the late 1880s in much the same way as the Canadian fishery, being dependent on adult fish to meet domestic needs and the demand for a dry-salted product in the Orient. From about 1920 onwards, however, the fishery followed a uniquely different course. Emphasis continued on adults, but primarily as bait for other commercial fisheries (halibut, cod, and dogfish) until the late 1940s after which the fishery transformed into one aimed almost exclusively at O-group juveniles to meet the requirements of a growing salmon sport fishery (Williams 1959). This activity predominated until 1957 when for the first time it became permissible to reduce adult herring to meal and oil, but in only two small localities within areas 80 and 82 (Trumble 1980). This fishery along with those supplying food for zoo animals and bait for recreational and other commercial fisheries raised production in the succeeding 15 yr to an average of 2500 t annually. Apparently because of weakening market conditions, fisheries for all but recreational bait declined after 1970 to a very low level in 1979. In their place, beginning in 1973, emerged the roe herring fishery similar to that already underway in British Columbia. Like the earlier reduction fishery, this one was restricted by legislation to a small area encompassing mainland inshore waters of area 80. Total production reached an all-time high of nearly 6000 t in 1975 but has declined to less than 3000 t in more recent years (Trumble 1980).

The discreteness of Washington herring stocks is probably reflected in the fact that there was little or no indication of a collapse concurrent with that which occurred in British Columbia during the late 1960s.

Future prospects — With a management policy that subscribes to exploitation considerably less than the biological or economic optimum in Canadian waters of the Strait of Georgia, it is assumed that there will usually be an unused surplus, barring natural disasters or say a massive oil spill at time of spawning. However, it is possible that the current margin left for errors in prediction can be reduced by development of more reliable indicators of egg and larval survival and forecasts of spawning stock distribution and behavior.

Yet, with the growing political influence of recreationists, implementation of such refinements in management may never come to pass. There is widespread popular belief in (1) a positive relationship between herring spawning stock size (at all levels) and the resulting brood strength and (2) higher survival and better growth of chinook and coho salmon (sportfish) stocks when herring abundance is high. Neither of these contentions has been scientifically demonstrated (Taylor 1964; Healey 1976).

DOGFISH (*SQUALUS ACANTHIAS*)

Life cycle — The dogfish is a small shark notable for its abundance, slow growth rate, low fecundity, and longevity. At least 20 yr, possibly as many as 35, are required to reach maturity and some individuals probably live considerably more than 70 yr (Ketchen 1975). The female gives birth to a litter of six or seven pups after a gestation period of close to 23 mo, a term unique to the vertebrate kingdom (Ketchen 1972). Thus, the species has both a low reproductive rate and low growth rate.

Young dogfish begin their life in midwater. Beamish et al. (1982) found dogfish of 1–6 yr old to be most abundant in or above scattering layers in the Strait of Georgia at depths of 100–170 m.

In early life, food consists mainly of invertebrates but as age advances the diet changes to predominantly fish and large invertebrates. At the same time, older, adult fish become more closely associated with the continental shelf where they are caught with trawl nets, long-lines and (formerly) with sunken gill-nets. However, schools are occasionally found in shallow or even surface waters.

Stocks — Results of preliminary taggings conducted along the east coast of Vancouver Island from Deep Bay to Sidney (Saanich Peninsula area) showed considerable wandering not only along the east coast but movements across the deep water of the Strait to banks off the Fraser River Estuary and to United States waters of the Strait (Foerster 1942).

More recently, substantial taggings in the Canadian portion of the Strait of Georgia have confirmed the strong tendency to wander within that area but also into the United States portion and northern waters of Puget Sound. Small numbers of tagged fish have been recovered in Juan de Fuca Strait and off the west coast of Vancouver Island (Brown et al. 1979; Beamish et al. 1981; McFarlane et al. 1982).

United States tagging has been conducted in various sections of Puget Sound, the United States portion of the Strait of Georgia, as well as on Swiftsure Bank at the western Entrance to Juan de Fuca Strait. Results from all taggings combined, as reported by Fujoka et al. (1974), showed that only 2% of all tag recaptures were made in Canadian "inside" waters but 12% if we consider only those taggings conducted in United States waters of the Strait of Georgia (statistical area 80 in Fig. 1). Substantial numbers of dogfish tagged on Swiftsure Bank found their way into both the Canadian and United States portions of the Strait of Georgia and Puget Sound.

It is apparent that the proportions of Canadian and United States tags recovered in the other country's waters is a function of time and distance from the international boundary and that the same applies to the relationship between dogfish of Georgia Strait and those found seasonally in Juan de Fuca Strait. Thus, for present purposes it is necessary to presume that dogfish in the Canadian and United States sections of Georgia and Juan de Fuca straits and Puget Sound represent a single stock probably consisting of several subunits. Even this loose definition is not sufficient to accommodate the imprecise account of the fishery that follows.

History of the fishery — The fishery for dogfish in British

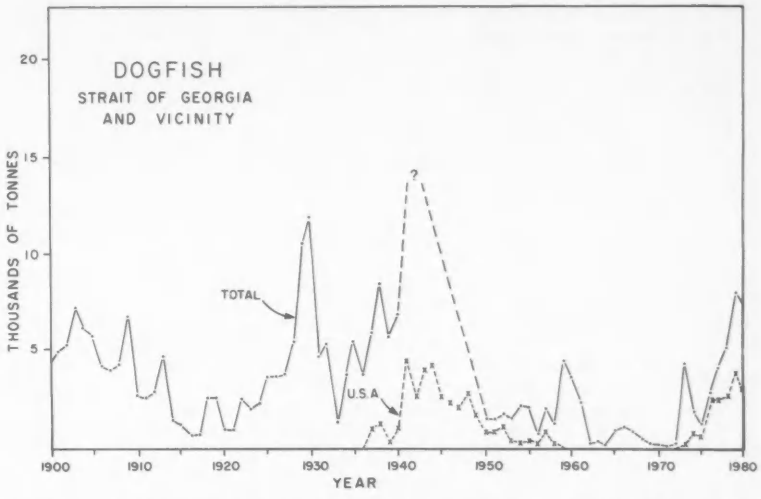

FIG. 4. Round weight or estimated equivalent weight of dogfish caught by commercial gear in the Strait of Georgia and adjacent inshore waters of Canada and the United States.

Columbia waters has had a long and varied history undergoing periodic surges of industrial importance interspersed with periods when the species was regarded as a curse and nuisance to the pursuit of fisheries for other species. Extensive use of the liver and body oil of dogfish by native indians was first noted by Lord (1866). First commercial production for both domestic and export markets amounted to 180 000 gal. (1 gal. = 4.55 L) of oil (about 5000 t of whole fish) in 1877 (Anderson 1877). High-quality liver oil found ready use as a lubricant for forestry machinery and skidroads, coal mining facilities, and ships' engines. The oil was also extensively used for lighting purposes and was the fuel source for at least two lighthouses. Numerous "oileries" and reduction plants were present in the Strait of Georgia prior to 1900. After the turn of the century dogfish liver oil was largely replaced by other oils in industry and advent of the calcium carbide lamp was a major contributor to the decline shown in Fig. 4 during the period 1900–15 (Taylor 1916).

There followed a period of low production accompanied by pleas from fishermen for eradication of dogfish because of damage done to gear and to other more desirable species. A short-lived attempt to market dogfish as a foodfish in the United States ended in 1918.

Although the use of dogfish for fishmeal and fertilizer began around 1892 (Barraclough 1948a), it did not become an important source of income until the early 1920s. Immediately thereafter the market demand shifted to fish oil and meal. Production in the Strait of Georgia reached a peak of 4000 t (equivalent to nearly 12 000 t of whole fish) in 1930 following which there was a sharp decline associated with the Great Depression.

In the middle to late 1930s, production rose again, still with emphasis on fishmeal and oil. It is uncertain to what extent the industry in inshore waters of the state of Washington paralleled that in Canada because the state did not begin publishing figures until 1937. Fiedler's (1929) review of Washington fisheries suggests that dogfish landings were either negligible or nonexistent from 1888 to 1928. The Washington fishery, beginning as it appeared to in 1937, was presumably the forerunner to the most spectacular period in the history of the fishery.

While the presence of high concentrations of vitamin A in dogfish liver was discovered in the late 1920s (Brocklesby 1927), it was not until the early 1940s that a strong demand arose to offset shortages from traditional (cod) fisheries in the North Atlantic.

The state of Washington apparently was able to keep track of dogfish liver production from inshore waters throughout the critical years 1941–49 (DiDonata 1974), but in Canada, this differentiation could not be maintained. By the early 1940s, larger vessels (from a rapidly expanding trawl fleet) were making deliveries from areas outside the Strait. Thus, the broken line in Fig. 4 represents little more than a guess at combined Canadian and United States removals in the 1940s, guided by anecdotal information that the fishery reached a peak in 1941 as opposed to 1944 in more distant waters.

The fishery was pursued not only with traditional long-line gear but also by the expanding use of trawl-nets. Sunken gill-nets, which had been introduced as far back as the early 1920s, were alleged to be interfering with reef species such as the lingcod (*Ophiodon elongatus*) and were banned from the Strait of Georgia in late 1944 (Barraclough 1948a). Full attention was now being directed to the liver market; rendering of carcasses to fishmeal ceased to be an economically viable operation and the last of the dogfish reduction plants, one in Deep Bay and the other on one of the Gulf Islands, were closed in 1944.

By the middle 1940s there was no question that the

abundance of adult dogfish (those possessing livers with highest vitamin A potency) had been greatly reduced in numbers not only in the Strait of Georgia but also in more distant waters of Hecate Strait (Barraclough 1948b). Conservation measures for dogfish were proposed at regional and international meetings. However, by 1946, renewed competition from Atlantic sources weakened the market. Collapse of the fishery came in 1950 with importation of inexpensive vitamin A oils from Japan and the development of a synthetic product.

As shown in Fig. 4, sporadic low-level activity occurred in both the Canadian and United States fisheries during 1950–72. From 1958 to 1961 the Canadian government introduced small subsidies to encourage resumption of fishing, in response to renewed and growing complaints of interference of dogfish with other fisheries and damage to gear.

From 1972 to the present, a substantial fishery resumed in both Canadian and United States waters, this time to supply foodfish markets in Europe where dogfish were in short supply. The market takes only large relatively old dogfish and catches are made with long-lines more than with other gears. In the Canadian portion of the Strait, Fisheries Management has imposed a trial total allowable annual catch of 3000 t. It is still too early to say whether the inshore stock(s) can withstand this level of removal along with that occurring in United States waters.

Future prospects — The current fishery for dogfish is probably of sufficient magnitude to reduce substantially the adult component of the stock(s). In consequence, a reduction in recruitment can be anticipated, but its effect, if measurable, is decades away. Besides, there is some basis for believing that a compensatory rate of natural mortality is the principal mechanism of population control. In other words, as exploitation increases, density decreases and this in turn leads to a reduction in natural mortality (presumably of young juveniles) (Wood et al. 1979).

The adult component forms a relatively small fraction of the total dogfish biomass, probably less than 20%. Thus, the immediate benefits to other fisheries, in the form of reduced interference and damage to gear, is likely to be slight except in very localized areas inhabited by adults.

Even if there were known factors in the environment that have impact on the survival of young, the stock contains so many age groups that any alteration of its stability would be unmeasurable.

LINGCOD (*OPHIODON ELONGATUS*)

Life cycle — The lingcod is unique to waters of the Northeast Pacific along with other members of its family Hexagrammidae (greenlings). Individuals commonly grow to more than 1 m in length. Wth a large head and a mouth heavily arrayed with "canine" teeth, the lingcod not surprisingly is a voracious feeder on other fishes. It lives on the continental shelf frequently associated with reefs, reaches maturity in 4–5 yr, and forms prespawning aggregations in the autumn. Spawning occurs primarily during December to March, at least some of it in shallow water close to the intertidal zone where eggs are laid in large adhesive masses under rocks or in crevices. Survival of eggs appears to be greatest in localities of high tidal velocity (Giorgi 1981). It remains uncertain whether spawning also occurs where the species dwells on offshore reefs (depths to 140 m) and where tidal velocity (in the Strait) is low.

The male lingcod assumes a territorial behavior prior to spawning and stands guard over the egg mass, fanning it (according to Hart 1973) with its large pectoral fins. Fanning was not noted by Low and Beamish (1978) or LaRiviere et al. (1981), but such behavior may not occur where current velocities are naturally high. In any event, Low and Beamish (1978) believe that the protective role of the male is vital to the welfare of the young. During this period the male is highly vulnerable to capture by man and other large predators.

After hatching, the young become distributed in the water column (Phillips and Barraclough 1977) but within a few months, they assume a demersal existence. By 1 yr of age, many are to be found on sand bottom to depths of 80–100 m. In the Strait of Georgia, lingcod tagged from hand-line (reef fishing) vessels tend to be recaptured by those vessels, while those tagged from trawlers tend to be recovered by the same gear. The former are usually larger and older than those caught by trawls; hence, there is a suggestion that once they move to rocky areas or reefs, lingcod become relatively invulnerable to trawls (Chatwin 1954).

Stocks — Results of tagging conducted in the Strait of Georgia (Hart 1943; Chatwin 1954) suggest that lingcod lead a rather sedentary existence once they reach adulthood. A rather remarkable case in point was the recapture of a tagged lingcod after more than 12 yr at liberty on virtually the same fishing spot where it was released (Anonymous 1954). There are no well-defined migration patterns although such behavior may be more common elsewhere. It is presumed that in the Strait there are numerous localized populations that can be regarded as a single stock for management purposes (Stocker 1981).

History of the fishery — Until 1927, lingcod appeared in fishery statistics under a "cod" category, but there is reasonable assurance from remarks of Wilby (1937) and earlier comments of Taylor (1915, 1916) that lingcod, rather than true cod (*Gadus macrocephalus*) and misnamed species such as blackcod and rockcod, comprised almost all of the catch prior to that time. The principal means of fishing, no doubt adapted from native indian methods, was by hand-line or jigging.

As shown in Fig. 5, production from the Strait of Georgia rose from small beginnings after the turn of the century to more than 4500 t in 1936. Uncertainty attends the amount of lingcod landed during the 1940–50 period for reasons already given, but during this period all landings in southern British Columbia reached a maximum of no more than 3600 t.

When it was once again possible to obtain reliable records of the fishery in the Strait (1951), the catch had fallen to 1300 t and this decline has continued to the present.

There is little doubt that the fishery from the mid-1930s through the war years had heavy impact on the stock. Lingcod were pursued with line, trawl, and gill-net gear as much for their high-priced liver as for food. However, the continued decline through the 1950s to 1980 cannot be fully explained.

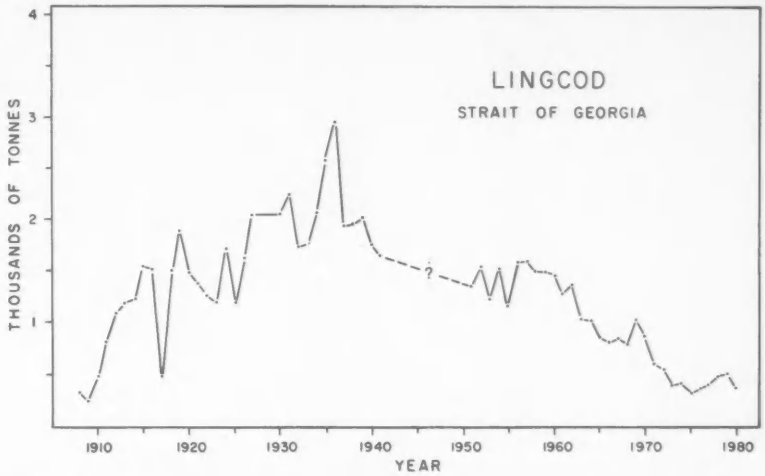

FIG. 5. Canadian landings of lingcod caught by all commercial gear in the Strait of Georgia (minor statistical areas 13–20 and 28–29) (see text for details).

Catch declined in step with reported days fishing to 1975, probably in response to socioeconomic conditions, but recent (1977–80) indications of greatly intensified fishing with no appreciable increase in catch suggest that low abundance is a limiting factor (Stocker 1981). The advent of recreational scuba diving and spearfishing has been suggested as a major factor, especially with respect to destruction of male fish during the highly vulnerable nesting stage. Another factor may be predation due to the marked buildup of sealion and hair seal populations in the Strait. Finally, over a more protracted term, destruction of juveniles by trawl nets may have had greater impact than earlier believed (Ketchen 1950).

Returning to the spearfishing factor, heavy mortality among male lingcod could act two ways to affect the commercial fishery, either directly (by their removal) or indirectly through increase in egg mortality and subsequent reduced recruitment. The latter view holds only if it can be correctly assumed that the bulk of lingcod spawning occurs within the depth range frequented by most scuba divers. A winter (December, January, and February) closure to commercial fishing in the Strait was in effect as early as 1940, but recently (1980), the closed season was extended to apply from November 15 to April 15 and to all types of fishing including recreational gear.

Future prospects — The lingcod is a valuable commercial species and attracts recreational fishing, especially when salmon are not plentiful. Whether or not future production can be restored to former heights depends on research to determine what factors are responsible for current stock conditions and adoption of appropriate corrective measures.

OTHER GROUNDFISH

Background — To this point we have considered fisheries that have been directed at particular species. There is another group of groundfishes that, because they cannot be exploited efficiently without the use of the otter trawl or bottom-drag nets, are the object of a mixed or at best a less-directed fishing operation. This complex group of species, all with uniquely different life histories, include foremost the Pacific cod (*G. macrocephalus*), several flatfishes (Pleuronectidae spp.), walleye pollock (*Theragra chalcogramma*), dogfish, and several others. The fishery for these species deserves general comment before we consider a few in more detail.

The trawl fishery for groundfish began in the Strait of Georgia around 1912 in the immediate vicinity of Vancouver (English Bay, Point Grey) and soon spread to grounds off the Fraser River Estuary from the North Arm to Point Roberts, presumably with primary interest in English or lemon sole (*P. vetulus*) and Pacific cod. It then expanded to waters among the Gulf Islands and by the late 1920s and early 1930s had covered most of the fishing areas along the east coast of Vancouver Island from Sidney to Comox. All fishing grounds were within the depth range of 25–110 m.

The rapidly increasing value of dogfish liver, as previously mentioned, was largely responsible for an expansion of the trawler fleet during the 1940s. This kind of fishing was most unpopular with traditional hand- and long-line fishermen as well as with sport fishermen. Alleged interference with the lingcod fishery prompted a closure to trawlers of numerous small areas within the Strait from 1941 to 1946. Suspected overfishing of lingcod, dogfish, and of other species (e.g. Pacific cod) that could be caught efficiently with no other type of gear led to a major closure based on recommendations contained in a special memorandum (Hart 1946). This denied trawlers access to all but the southerly part of the Strait of Georgia including grounds off the Fraser River Estuary.

Subsequent biological investigations indicated that substantial resources of flatfishes, Pacific cod, and other species

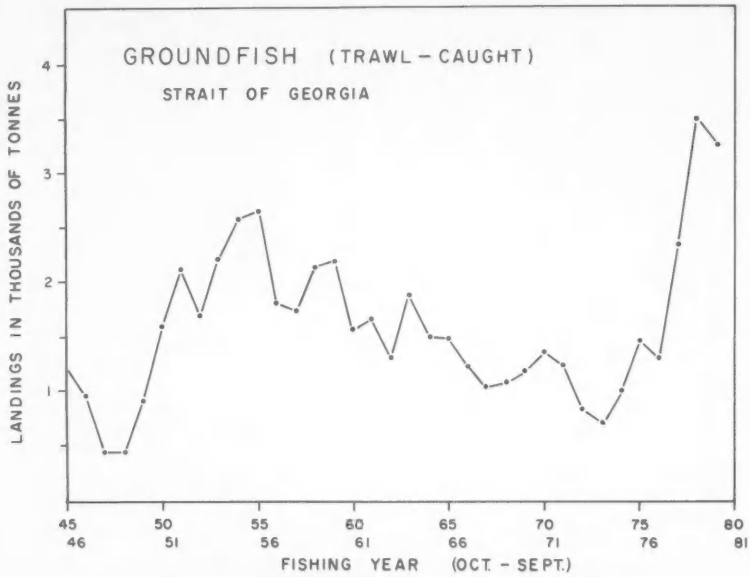

FIG. 6. Canadian landings of trawl-caught groundfish (other than dogfish) from the Strait of Georgia (minor statistical areas 13–20 and 29; fishing year October–September).

would be wasted if the areas remained closed indefinitely. Furthermore, it seemed unlikely that incidental catches and inadvertent destruction of juvenile lingcod was a major threat to the lingcod resource (Ketchen 1950). Accordingly, areas were reopened on an "experimental" (seasonal) basis between 1948 and 1952. Further details on this and later phases of the trawl fishery in the Strait have been provided by Forrester and Ketchen (1963), Forrester and Smith (1974), and Westrheim (1980).

Detailed documentation of the trawl fishery did not begin until 1945 at which time use of logbooks followed by a interview system provided information on the fishing areas and amounts of each species caught.

A composite of the production of about 12 groundfish species exclusive of dogfish is given in Fig. 6. A number of events are highlighted by this figure: (i) the low catch level in 1947–48 and 1948–49 was due to the aforementioned closure of many productive areas in the Strait; (ii) from then until 1952–53 marked the period of unusually large catches of English sole (*P. vetulus*) and rock sole (*Lepidopsetta bilineata*) that had accumulated during the period of closure; (iii) during 1954–59, Pacific cod predominated among the foodfish, along with relatively heavy landings of pollock used at that time as animal food by fur-farm ranches; (iv) from 1960 to 1973, the fishery followed an irregular downward course and depended primarily on catches of Pacific cod and flatfish; (v) after 1973 there was a resurgence of the fisheries for cod and flatfish as prices caught up with rising costs of fishing, but more important, pollock came into its own as a foodfish for human consumption and was the object of a distinctly new fishery pursued chiefly with midwater trawls. Now at a record high of over 3600 t/yr, this production includes some landings of another midwater or pelagic species, the Pacific hake (*Merluccius productus*), about which more will be said in a subsequent section (New Fisheries in the Strait of Georgia).

For more detailed consideration of events in the trawl fishery, we shall select Pacific cod and English sole, since they have been the long-term albeit variable supporters of the Strait of Georgia fishery. The former comes closest to being the object of a directed fishery, while the latter, particularly in the last two decades, has tended to be a by-catch of the cod fishery.

Pacific cod (Gadus macrocephalus) — Life cycle — In the Strait of Georgia the species is close to the southern limit of its North Pacific range and appears to avoid areas where sea temperature rises above 10°C. Laboratory studies show that eggs and larvae are adversely affected under such conditions (Alderdice and Forrester 1971).

Spawning takes place in midwinter at depths of 55–90 m. At least one important spawning ground in the Strait is to be found at Nanoose Bay, from which cod disperse mainly to the southern part of the Strait (Westrheim 1982). Other spawning grounds may be in the Hornby Island–Cape Lazo area in the northern half of the Strait and in Swanson Channel in the south. The eggs are demersal and slightly adhesive. Larvae and young juveniles probably inhabit moderate depths but are occasionally found in inshore waters.

Pacific cod are fast growing, mature at an age of 2–3 yr, and very few appear to live beyond 5 or 6 yr (Ketchen 1961).

Stocks — Results of tagging in the Canadian sections of the Strait of Georgia and Juan de Fuca Strait (Westrheim 1982)

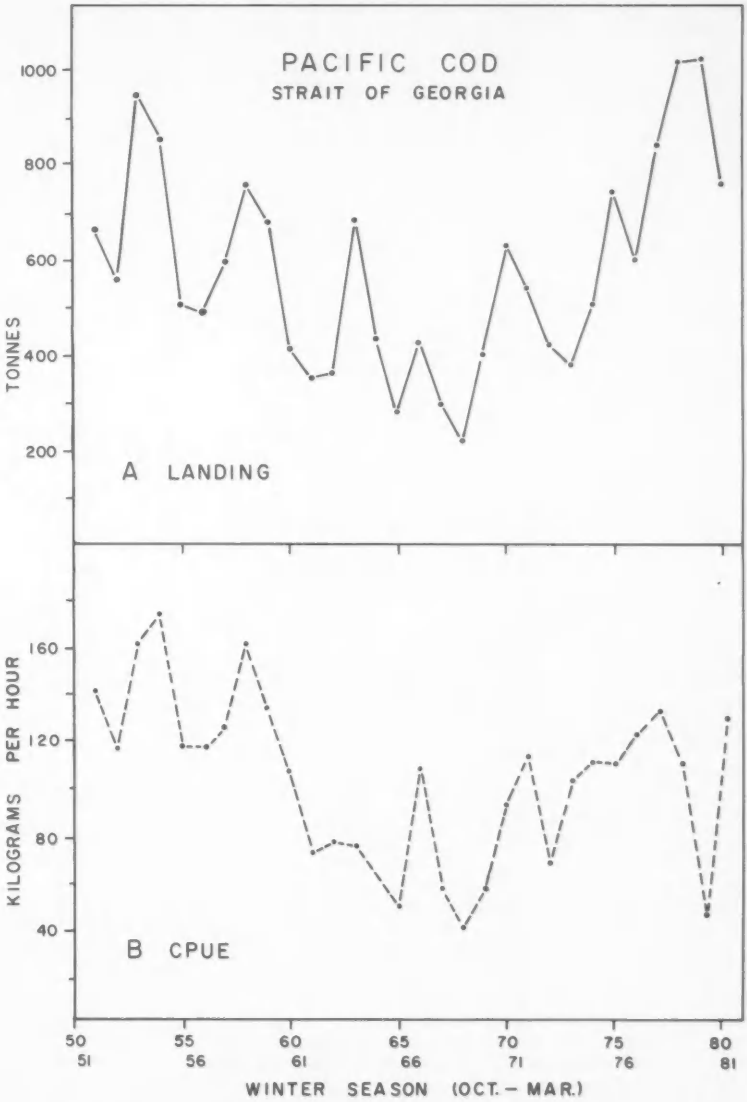

FIG. 7. (A) Canadian landings of Pacific cod from the Strait of Georgia during the winter (October–March) trawl fishery. (B) Corresponding CPUE based on total foodfish fishing effort as estimated by Ketchen (1979) and subsequently modified (minor statistical areas 13–20 and 29) (see text for details).

and in corresponding United States waters (Gosho 1976) reveal extensive intermingling within and between those regions and some interchange with cod occurring off the west coast of Vancouver Island and northwestern Washington. Of special note is the strong association between cod that spawn in Nanoose Bay and those taken from United States areas 80 and 82 (Fig. 1). The presence of more than one spawning population suggests that there are several intermingling units but the interrelationships cannot be quantified.

History of the fishery — A trawl (and possible line) fishery for

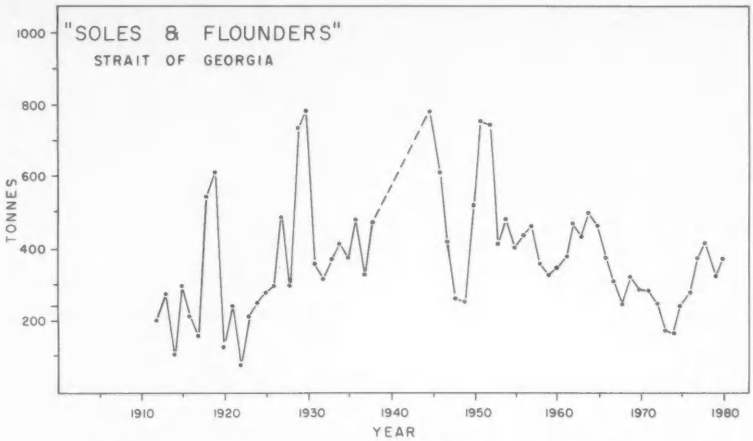

FIG. 8. Canadian landings of various species of flounders (*Pleuronectidae*) from the Strait of Georgia (minor statistical areas 13–20 and 29, or earlier equivalent).

Pacific cod developed in the 1930s, reaching a peak of about 800 t in 1938. By 1941 and 1942 when south coast landings would have included some catches from other areas, production had dropped substantially, possibly giving rise to fears that stocks in the Strait were overfished, which was one of the reasons given by Hart (1946) for the closure of many grounds to trawling. At that time the fact that cod undergo substantial natural fluctuations in abundance was not known.

When a logbook and interview system was instituted in 1945–46 the estimated cod production from the Canadian part of the Strait was about 725 t or roughly the same as immediately before World War II.

As already indicated in the general comments (above), particularly low production in 1947–48 and to some extent as late as 1951–52 could be attributed to closed areas and restricted fishing seasons.

Trends in catch for the years 1953–80 were characterized by declining production to 1966 and rising production thereafter to an all-time peak of 1600 t in 1980. Superimposed on these trends were short-term quasi-cyclical fluctuations for which Pacific cod in British Columbia waters are noted and appear to be due to natural causes (Stocker 1981, p. 175).

Essentially the same sequence of events is shown in Fig. 7, although depicting production for the winter season (October–March) only. Accompanying these catch figures are corresponding estimates of catch per unit of effort (CPUE) for a standard class of trawlers (from Ketchen 1979) but subsequently modified to account for a long-term increase in efficiency (K. S. Ketchen, unpublished data). The CPUE graph indicates that, with some exceptions, especially in the last 3 yr, the long-term and short-term fluctuations in catch were a reflection of changes in abundance–availability of cod. Changes in catch appear to be largely independent of Canadian fishing effort. However, a definitive conclusion cannot be drawn without information on age composition of the catch and the impact on the Canadian fishery of variations in removals from the United States sector of the Strait.

Future prospects — Until overfishing can be positively identified, it must be presumed that fluctuations in abundance are predominantly of natural origin. Discovery of the mechanism(s) may enable prediction of these fluctuations, for the benefit of both industry and management.

In Washington State, a substantial recreational fishery is developing, and this pastime eventually may be adopted in a few localities in Canadian waters close to major population areas.

Flatfishes or flounders (Pleuronectidae) — In the trawl fishery of the Strait of Georgia, production of flatfish is predominated by that of English sole, followed by rock sole (*L. bilineata*) and starry flounder (*Platichthys stellatus*). Combined, the yield is a small fraction of that of Pacific cod.

Life cycles — Spawning of these flatfishes differs slightly by species but falls within a depth range of 20–90 m in midwinter. Both the English sole and starry flounder produce a highly buoyant egg that rises to the sea surface. Larvae carried to sandy intertidal zones metamorphose and settle to the bottom where they remain until late summer. They then move to subtidal waters and over the succeeding 2 or 3 yr descend to depths ocupied by adults.

The rock sole, in contrast, produces an ahesive egg in consequence of which the larvae and metamorphosed young probably remain in the general depths occupied by their parents (15–30 m). Like the other species, they take 3–4 yr to reach sexual maturity and marketable size.

Stocks — In the Strait of Georgia, extensive tagging has revealed the presence of at least three stocks of English sole: one occupying the Vancouver Island coastal waters from Parksville to Comox, another in waters amongst the Gulf Islands from Nanaimo to Sidney, and a third in the vicinity of Burrard Inlet–Point Grey running southward into United States waters of the Strait. Within each of these areas there are seasonal movements associated with spawning.

Recaptures of tagged individuals in waters off the open

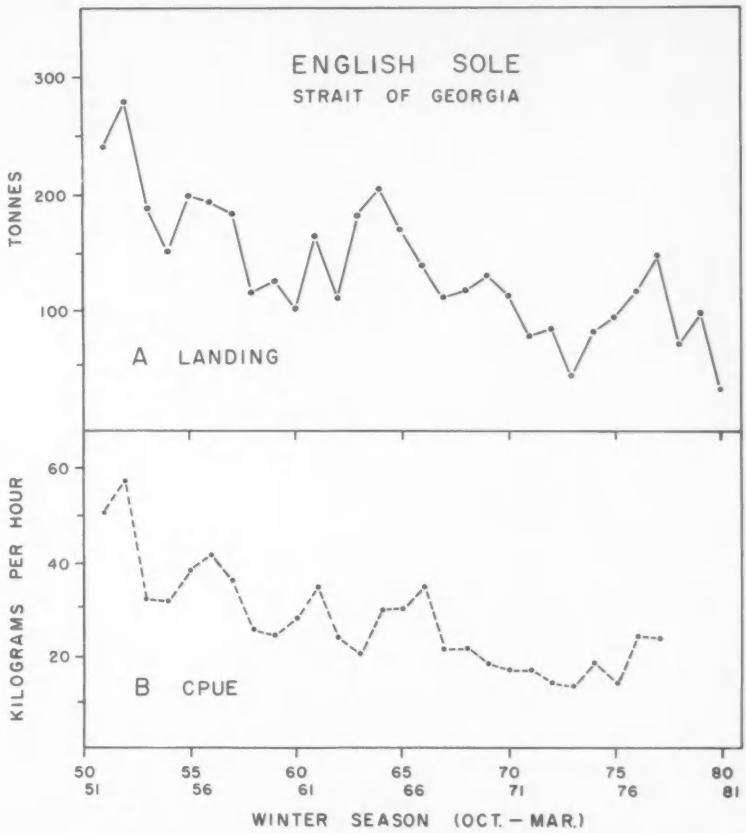

FIG. 9. (A) Canadian landings of English sole from the Strait of Georgia during the winter (October–March) trawl fishery. (B) Corresponding CPUE (minor statistical areas 13–20 and 29) (see caption to Fig. 7).

coast from southwest Vancouver Island southward as far as Eureka, California (a net distance of nearly 1000 km), were primarily from taggings conducted in the summer and early autumn. This led Ketchen and Forrester (1955) to postulate that in addition to the three relatively distinct resident stocks, there is a highly migratory element that invades the Strait in summer and returns to the open coast in late fall.

Too little tagging of rock sole and starry flounder has been done to shed light on their movements in the Strait of Georgia. Observations elsewhere (Hecate Strait) suggest the rock sole is less mobile than the English sole and probably exists as numerous small populations around the periphery of the Strait, where depth and bottom composition meet its requirements for feeding and reproduction. Manzer's (1952) summary of starry flounder tagging conducted elsewhere indicated little movement. The same may apply in the Strait of Georgia.

History of the fishery — The history of the fishery for flatfish in the Strait, from its beginning in 1912 through the 1930s, follows that already provided in the background remarks above.

The historical record of flatfish landings (recorded as "soles and flounders" in the Dominion Bureau of Statistics) shows unstable production from the onset of fishing to the mid-1930s, due presumably to economic conditions (Fig. 8). As was the case for other species already considered, landings from the Strait during the late 1930s to 1945 were confounded by landings from other areas; thus, nothing can be said about production during this period except that it was one of peak activity for trawlers.

Again, the low level of catch in 1946–49 reflected the impact of extensive closures, and high removals in 1951–52 were from stocks that had accumulated during these closures (Forrester and Ketchen 1963). Thereafter, production followed an irregular downward course to 1974, with a modest increase in more recent years.

A closer look at the catch of English sole alone is provided in Fig. 9, using the same 30-yr span of winter fishing seasons (October–March) as used for Pacific cod. To arrive at an index of abundance, we have used the same effort as that used in computing Pacific cod CPUE, presuming that English sole was primarily a by-catch of the cod fishery.

Flatfishes and particularly English sole responded rapidly to the broad closure of fishing in the late 1940s. High catch and CPUE in the early 1950s are a reflection of this benefit. Since that time, despite continued restrictions on fishing season in the northern half of the Strait, both production and CPUE have followed a long-term decline. Ketchen (1979) suggested that a recovery might have been in progress in years after 1973–74 but advised caution in the interpretation of CPUE in a by-catch fishery and in the absence of information in changes in efficiency. Since that time, the efficiency factor has been at least partly quantified (K. S. Ketchen, unpublished data), and as shown in Fig. 9, apparent stock size has continued to decline. Possibly both "growth and recruitment overfishing" (as defined by Cushing 1977) are in progress.

An alternative explanation, with persuasive supporting evidence, is that pollution of the inter- and sub-tidal habitat occupied by 0- and 1-yr age group English sole has greatly increased the mortality of these young juveniles and hence reduced recruitment to the fishable stocks. The incidence of skin papillomas on these fish in the Strait of Georgia and Puget Sound is inversely related to the distance from major urban centers, the sources of carcinogenic contamination (Stich et al. 1977). Off the Fraser River Estuary where concentrations of pollutants of all kinds would be expected to be greatest, the long-term decline in catch of English sole has been more rapid than in other parts of the Strait.

Future prospects — Presuming current overfishing, it seems unlikely that the condition of flatfish resources will improve without a substantial reduction in effective fishing effort and that the fleet will come to depend on other, less desirable species (Dover sole, *Microstomus pacificus*, and turbot, *Atheresthes stomias*), a process that appears to have already begun. However, further restriction on the fishery poses a problem not uncommon in the management of multispecies fisheries: Pacific cod, the dominant species in the bottom-trawl fishery, apparently is in no need of restriction at the present time. Thus, restriction of effort would lead to underutilization of that species.

Dungeness Crab (*Cancer magister*)

Life cycle — The Dungeness crab occurs throughout the Strait of Georgia in tidal and shallow subtidal (to 100 m) habitats where there is firm sandy bottom. Following mating in summer months, as many as a million eggs are spawned and retained on the abdomen of each female until hatching late in March to early April. The larvae are pelagic until about July, passing through six stages of development. In all but the last of later stages they become photonegative and descend from near surface to deeper layers. Prior to settling on the bottom, the last stage or megalops, being photopositive, swims at the surface to take advantage of onshore drift currents (Lough 1976).

Growth is accomplished by frequent moulting of juvenile crabs (10 times in 2 yr), but following attainment of maturity at 3 yr, moulting takes place annually or sometimes less frequently. Commercial size of male crabs is reached in 4 yr. Because females grow slower after the 3rd yr, few reach legal size (Butler 1960, 1961).

Stocks — There are two, possibly three, main stocks of Dungeness crab in the Strait. One is defined by fishing grounds extending from Roberts Bank and Sturgeon Bank at the mouth of the Fraser River to Boundary Bay and for an uncertain distance southward into United States waters of the Strait. Another occurs along the east coast of Vancouver Island from Sidney to Nanaimo, while a third is to be found in Burrard Inlet near Vancouver.

History of the fishery — Commercial fishing is conducted primarily with traps, and the most productive fishing season is from May to October. The species is also the object of a recreational fishery.

Dungeness crab catches were first recorded in 1885 and likely originated from Burrard Inlet near Vancouver and Esquimalt Harbour near Victoria. By the early 1900s, fishing had spread to Boundary Bay and Nanaimo Harbour (Weymouth 1915). By 1940, annual production from the Strait of Georgia reached 334 t.

More detailed information on the commercial fishery became available with the introduction of the previously mentioned sales slip system of recording landings in 1951. Total production from the Strait in that year was 387 t, achieved by approximately 5800 d of fishing (Fig. 10). While days fishing as a measure of fishing effort may be misleading because it takes into account neither the number of traps fished nor periods between lifts, a wholly reliable indicator of abundance is precluded. Nonetheless, general trends may be indicative of changing availability and/or abundance.

From 1951 to 1957, landings followed the trend of effort (particularly after 1954) and by 1960 had increased greatly to 407 t, a figure disproportionately higher than the rise in fishing effort. An unusually consistent level of fishing effort occurred from 1960 to 1973, during which time landings rose to a record 544 t in 1965 and then declined, thus suggesting varying availability, if not abundance. After 1973, crab production rose sharply to 490 t, and again, this was attributable only in part to increased fishing days. From 1976 to 1980, catch remained relatively stable in the face of a marked upward trend in effort.

Dungeness crab, as a by-catch of the trawl fishery, was formerly of some significance off the Fraser River (90 t in 1953) but declined with the withdrawal of trawling effort in that area (Westrheim 1980). Today, small by-catches (2–5 t) are made principally in the Gulf Islands area.

In an attempt to relate apparent variations in crab availability to ocean conditions, use has been made of sea surface temperature data at Entrance Island. Uncertainty about the quality of fishing effort would make a statistical analysis pretentious, but there is a tendency for crab trapping to be good during warm summers (e.g. 1958, 1961, 1965, and 1967) and poor in cool summers (e.g. 1954, 1955). There is also an association between warm springs–early summers (and/or warm winters) and good fishing 4–5 yr later

FIG. 10. Canadian commercial (trap) landings of Dungeness crabs from the Strait of Georgia (minor statistical areas 13–19 and 28–29), with fishing effort as recorded on sales slips.

(e.g. 1958 compared with fishing success in 1962–63 and 1963 compared with 1967–68). Conversely, below-average temperatures of 1950 and 1974 were associated with poor fishing in 1954–55 and 1979. There is, of course, some confounding of effects of temperature (or associated factors) on catchability ("trapability") and recruitment (e.g. in 1967), so the true response cannot be clearly identified in this qualitative appraisal.

Future prospects — The Strait of Georgia should continue to support productive crab fishing, but the sport or recreational share of the catch is likely to grow at the expense of the commercial fishery. The former is not easy to document, but a series of surveys was conducted in 1980 by Fishery Officer Wayne Loudon (DFO Field Services) from Burrard Inlet to Boundary Bay. He estimated the recreational catch to be 31 200 crabs (21 t) or 17% of the commercial harvest in the same region. This share is bound to increase and become a significant factor before the end of the present decade.

Because the Dungeness crab inhabits shallow tidal waters, it is potentially vulnerable to the growing threat of pollution, especially from the Fraser River, and loss of habitat through industrial development of estuaries. However, there is as yet no evidence of this, at least in gross catch statistics.

SHRIMPS AND PRAWNS (FAMILY PANDALIDAE)

Six species of shrimp, all belonging to the family Pandalidae, are exploited in the Strait of Georgia. In decreasing order of importance, they are *Pandalus jordani* (smooth pink shrimp), *Pandalus platyceros* (prawn or spot shrimp), *Pandalus borealis* (pink), *Pandalopsis dispar* (sidestripe), *Pandalus hypsinotus* (humpback), and *Pandalus danae* (coonstripe).

Life cycles — Life histories of the six species are quite similar. Mature animals breed in the fall and developing eggs appear on the pleopods of the female abdomen where they are held until hatching and release in February or March. Larvae are pelagic until about July.

Individuals of all species normally mature first as males, and after one or two seasons in that phase, they become females for a year or two (Butler 1980).

Several species (pink, smooth pink, and sidestripe) occur on mud bottom (27–128 m), while the prawn lives on rocky bottom (46–146 m).

Stocks — All species presumably occur as a number of stocks throughout the Strait of Georgia. Localized otter-trawl

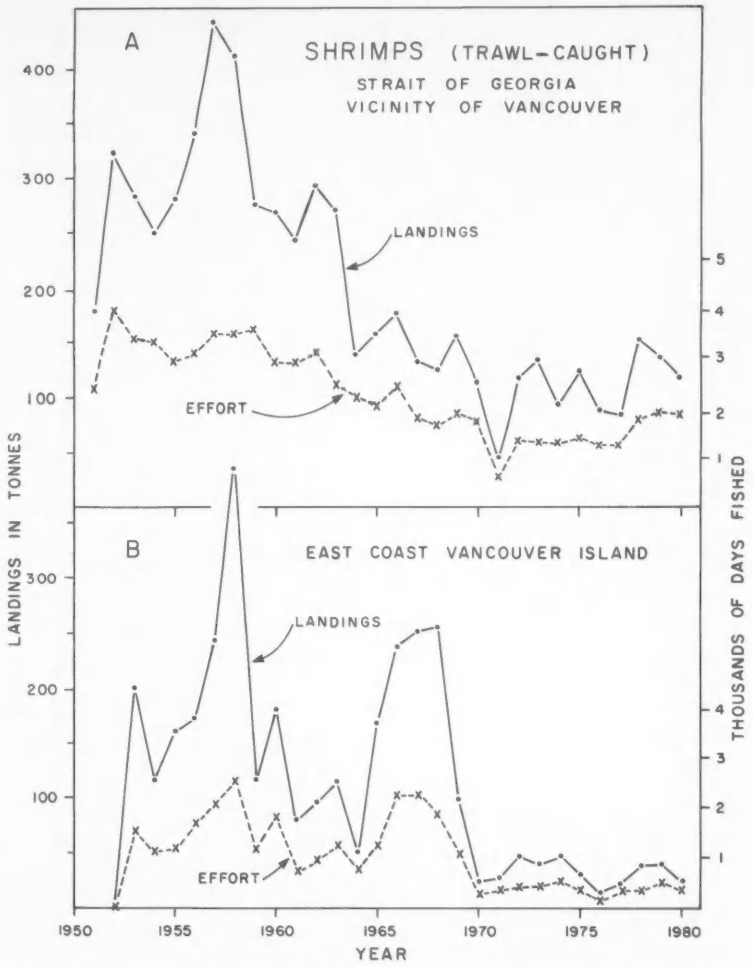

FIG. 11. Canadian trawl-caught landings of shrimps from (A) Vancouver area (minor statistical areas 28–29) and (B) the east coast of Vancouver Island (minor statistical areas 14 and 17), with fishing effort as recorded on sales slips.

and/or beam-trawl fisheries target on pink, humpback, and coonstripe shrimp in Howe Sound, English Bay, Burrard Inlet, and Indian Arm. On the east coast of Vancouver Island, the main species are smooth pink, sidestripe, and humpback, which are fished in two regions: from Comox to Parksville and from Nanaimo to Crofton (in Stuart Channel, part of the Gulf Island waters). Pink and sidestripe shrimp are trawled sporadically on the eastern side of the Strait near Welcome Pass.

Prawns are trapped commercially over most of the Strait, but the more important grounds in the southern part are at the entrance to Howe Sound, in Saanich Inlet, off Crofton, and from Gabriola Island to Parksville and in the northern part are off Little River, Hornby, and Lasqueti islands, Malaspina Strait, and on submarine ridges in the middle of the Strait such as Halibut Bank and Exeter Shoal.

History of the fishery — Early statistical records indicate that a shrimp fishery existed near Victoria before 1890. Contemporaneous operations probably occurred in Vancouver Harbour and inner Burrard Inlet. Trawling for pink shrimp reportedly began in English Bay around 1917. During the 1920s and 1930s most of the Province's shrimp production originated from the Vancouver (lower mainland) area.

Grounds along the east coast of Vancouver Island were not exploited until about 1953.

Records of catch and corresponding effort (expressed in fishing days) in these two regions have been maintained since 1951 and are illustrated in Fig. 11. In the Vancouver area, production mainly of pink shrimp was at a relatively high level from 1952 to 1963, reaching a peak of 442 t in 1957. From 1952 to 1971, effort apparently followed an irregular downward trend, but in more recent years both catch and effort have been relatively stable.

Fishing for smooth pink shrimp along the east coast of Vancouver Island had its beginning in Stuart Channel (Gulf Islands area) in late 1952 (Butler 1953) with a catch of merely 6 t. Yields rose rapidly to a peak of 402 t in 1958 and included landings from a ground near Comox that had come into production in 1954 (Butler and Legare 1954). Thereafter, there was a general decline, except for a resurgence in 1965–68 that can be attributed largely to an oscillation of effort between the east coast grounds and new ones found on the west coast of Vancouver Island (Barkley Sound).

Since 1971, possibly for economic reasons, fishing effort and production from the east coast grounds has remained at a low level. However, the possibility of low abundance cannot be ignored, since there have been periods in both the Vancouver and Vancouver Island area fisheries when recorded landings were disproportionately higher than recorded fishing days. This suggests that variations in recruitment have some effect on yield, but in the absence of age composition data, such a possiblity cannot be examined. Substantial natural fluctuations in abundance are well known in other shrimp fisheries along the North American coast (Geibel and Heinmann 1976), and there is no reason why they should not occur in inshore waters.

Still another possible factor in low catch levels is the as yet unsubstantiated practice of nonreporting of landings. Substantial but unkown quantities of shrimp probably are being sold directly to the public. This information loss has been confirmed with respect to the trap fishery for prawns. Only about one-third of pawn landings from the Strait of Georgia are recorded on sales slips (J. A. Boutillier, personal communication). For this reason, a review of the history of the prawn fishery would be incomplete and probably misleading.

Future prospects — Although overfishing does not appear to be a problem with respect to the trawl-caught species of shrimps, there is insufficient information to determine the underlying causes of the relatively low (reported) levels of catch and effort in the Strait. Recreational trapping of prawns is increasing in popularity and as long as catches go unreported, this will aggravate the current difficulty of assessing stock conditions and determining the needs for management.

OYSTERS (*OSTREA* AND *CRASSOSTREA* SPP.)

The only species of oyster indigenous to the Strait of Georgia is the native or Olympia oyster (*Ostrea lurida*). It was utilized by native indians and early settlers but commercial landings were not reported until 1884 (Quayle 1969a). The fishery continued until about 1936 when it collapsed because of overfishing, heavy mortalities after the severe winter of 1929, and the gradual development of a competing introduced species.

Two exotic oyster species were introduced into the Strait of Georgia, the eastern oyster (*Crassostrea virginica*) in 1903 and the Pacific oyster (*Crassostrea gigas*) from Japan in 1912 or 1913 (Quayle 1969a). The former did not flourish and, although a small residual population still exists in the Nickomekl River, which flows into Boundary Bay, it has no importance in the commercial or recreational fisheries.

The Pacific oyster is the only species commercially utilized at present. It has become well established in the Strait of Georgia (and elsewhere in southern British Columbia) and has become one of the dominant intertidal animals.

Life cycle — A water temperature of about 20°C is required for gonadal development and spawning of the Pacific oyster. At spawning, eggs and sperms are emitted into the water where fertilization takes place. The larval stage is spent in the upper 3–4 m of surface water and lasts 17–25 d depending on temperature. At the end of the pelagic period, the larvae seek out a clean hard surface, attach themselves to it, and remain there for life.

Being a subtropical animal occurring naturally between latitudes of 30–45°N in Japan, the species finds only marginally suitable ecological conditions in the Strait of Georgia for breeding. Water temperature and currents are rarely conducive to widespread breeding.

Seed importations and natural production — The first introductions were made in Ladysmith Harbour and Fanny Bay on the east coast of Vancouver Island by individual fishermen. This private activity continued for a number of years and by 1925, there was evidence that some breeding had ocurred at Ladysmith (Quayle 1969a).

First significant importations of small juvenile oysters (seed oysters) began in 1925. Between 1929 and 1932 approximately 4 million seed oysters were introduced, thus marking the beginning of the Pacific oyster industry in the Strait of Georgia and other south coast areas. Regular importations continued until 1962 and sporadically to 1977 (Fig. 12). The year 1951 marked the peak when 5400 cases representing about 81 million seed were received.

Following the first indication of a local natural set in 1925, the first significant breeding occurred in 1936 in Ladysmith Harbour. Spat were found at distances up to 80 km from this site (Elsey and Quayle 1939).

The first widespread breeding occurred in 1942 when summer sea surface temperatures in the Strait were well above normal. By that year, oyster culture was well developed and extensive populations of adults were present in many parts of the Strait. Spatfall was extensive throughout much of the Strait and even into many of the bordering mainland inlets. However, there was no spatfall north of Seymour Narrows or the Yuculta Rapids at the northern end of the Strait or at the southern end south of the Gulf Islands. Tidal turbulence and/or upwelling in these extremities of the Strait produce water temperatures that are too low to allow larval survival or successful breeding.

In 1958, another, and to date the largest successful breeding, occurred in southern British Columbia and again

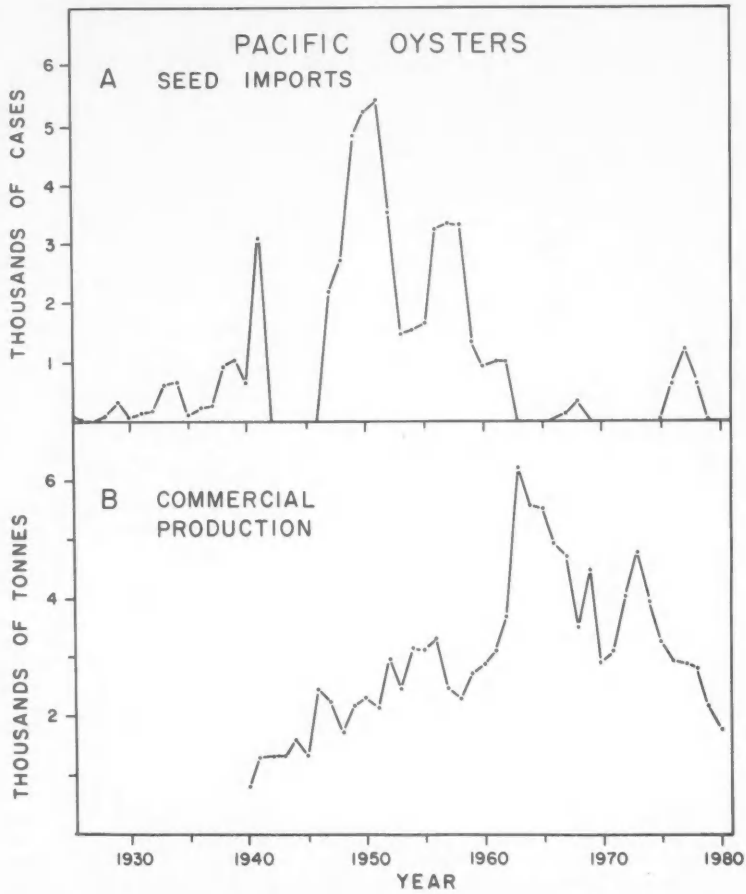

FIG. 12. (A) Imports of Pacific oyster seed and (B) commercial production (round weight) in British Columbia (mainly from the Strait of Georgia minor statistical areas 14–18).

was confined to the Strait of Georgia within the limits noted above. Another successful breeding occurred in 1961, with intensity similar to that of 1942. Since then, occasional local breedings have occurred but none had the intensity of those of 1942, 1958, and 1961.

Extensive as they were, these breedings were too erratic for the industry to have a dependable source of local seed and thus, reliance was placed on importations from Japan. In 1948, however, Pendrell Sound in the northeastern part of the Strait was found to have consistent breeding because of favorable local oceanographic conditions (Quayle 1974). In addition, an adjoining area, Hotham Sound, has been found to have fairly consistent breeding. By the early 1960s, the reliability of these areas had been accepted by industry. They now provide oyster growers in British Columbia with an inexpensive, reliable, and plentiful source of seed.

Industrial production — In the practice of oyster culture, intertidal bottom is leased by growers from the provincial government. Suitable areas are limited to little more than 1000 ha (Quayle 1969a). Seed is spread either directly on the growing grounds or held for a year on firm bottom high in the intertidal area (seed ground). After at least 3 yr, the oysters are ready for market.

Since 1940, production increased steadily from 789 t (round weight) to a peak of almost 6200 t in 1963 but has declined since then and in 1980 was slightly less than 1800 t (Fig. 12). Included in these figures is production from a new phase of the industry, oysters for the half-shell trade, which has risen from 22 467 dozen in 1974 to 41 353 dozen in 1980.

The extensive breedings in 1942, 1958, and 1961 had a marked impact on oyster farming practice. Large quantities of "wild" oysters were found in areas outside established leases.

Many growers harvested these oysters in addition to, or instead of, oysters from their leases. This accounted for the increase in production from the late 1940s to the peak in 1963. The necessity for planting seed was reduced and many growers no longer did so. Consequently, when the supply of wild oysters fell below commercial levels, production began to fall. Recent provincial legislation prohibits leaseholders from harvesting wild oysters except under permit. Before permits are issued, surveys are conducted to established harvest quotas.

Future prospects — The future of the oyster industry is promising, despite the limited amount of suitable bottom in the Strait of Georgia. Ideal conditions exist for off-bottom (floating) culture, a technique used extensively in Japan and Korea. Potential yield per hectare in off-bottom culture is about 25 times that of bottom culture.

CLAMS

For many years, only three species of intertidal clams in the Strait of Georgia have been the object of commercial and recreational fisheries: the butter clam (*Saxidomus giganteus*), littleneck clam (*Protothaca staminea*), and Manila clam (*Tapes philippinarum*). Other species occasionally enter the fishery, but the most notable recent development concerns the geoduck clam (*Panope generosa*), which is discussed in a separate section below (New Fisheries in the Strait of Georgia).

Life cycles — As a group it is difficult to generalize the life histories of clams, as, for example, sexual maturity is not so much a function of age as of size. Likewise, time of spawning varies depending on species and environmental conditions such as temperature. One species of horse clam (*Tresus capax*) in the Strait of Georgia spawns as early as February (Bourne and Smith 1972) and littlenecks as late as October (Quayle 1943). At spawning, which usually takes place en masse and may extend over a period of 1–3 mo, eggs and sperms are emitted into the water and fertilization takes place there. After hatching, the larval period is generally 3–4 wk. The larvae settle to the bottom and crawl (with a well-developed foot) until a suitable substrate is found where they attach themselves by a filament (byssus). They may or may not break free from this initial attachment, but usually when they are about 5 mm in shell length they burrow permanently into the substrate and remain there for life.

Growth rates are generally faster in the Strait of Georgia than elsewhere. Butter clams, for example, reach a commercial legal size (63-mm shell length) in about 5–6 yr.

Stocks — Particular stocks of clams have not been identified. However, because distribution of eggs and larvae depends greatly on the vissicitudes of wind- and tide-driven currents, it is not unreasonable to assume that there is one stock of each species and that distribution of each stock within the Strait is commensurate with the physical distribution of suitable substrates.

History of the fishery — The presence of large quantities of clam shells in middens around the Strait of Georgia attests to the fact that clams formed an important element of the diet of native indians long before the advent of white settlers. A commercial fishery by the latter probably developed in the late 1800s, but first official record of a canning operation in the Strait was in 1900 at Sidney, Vancouver Island. In the initial stages, clams were canned only during the off-season for salmon canning. However, the number of plants canning clams has never been large (Quayle and Bourne 1972).

Although records were maintained from 1900 onwards, landings by species were not recorded until 1951. At the beginning of the century, production for the whole coast was around 453 t, but by 1938 it had reached 3470 t. From 1938 to 1952 the landings fluctuated around a long-term average of 1400 t.

Production within the Strait of Georgia alone (Fig. 13) was slightly under 900 t in 1952, fell to little more than 300 t in 1959, and rose to more than 1000 t in 1972. Since then it has varied between 300 and 900 t.

Species composition of the landings has varied considerably, from 1951 to 1970 consisting mostly of butter clams, which are favored for canning. From then onwards, littleneck and Manila clams have predominated. This change reflected the strong shift in market conditions to "steamer" clams.

Major commercial production of butter clams has been from the east coast of Vancouver Island and Gulf Islands. These areas also produce considerable quantities of littleneck and Manila clams but substantial landings of these species come from the northern and eastern parts of the Strait.

Large annual fluctuations in landings have been due to a number of factors among which are socioeconomic conditions, availability of other work, pollution, and in some instances reduced abundance due to overfishing.

A recreational fishery has existed for many years but has grown substantially in recent years, particularly among the Gulf Islands and along the east coast of Vancouver Island. Beaches within easy access are heavily and probably excessively exploited.

Bivalves are efficient filtering animals and can filter out bacteria and virsues. Clams harvested from polluted waters have been known to transmit typhoid and infectious hepatitis to humans. Accordingly, regulations exist and widespread surveillance is maintained to ensure that clams are harvested in only approved areas. Numerous beaches in the Strait are closed because of pollution and this increases the harvesting pressure on clam populations in open areas.

Another problem that seriously affects clam fisheries in British Columbia is periodic outbreaks of paralytic shellfish poisoning (PSP), a condition that occurs when bivalves feed on *Gonyaulax catenella* or *Gonyaulax acatenella* (Quayle 1969b). Compared with other areas of the coast, PSP is not a major problem in the Strait of Georgia. However, there have been occasional major outbreaks such as in 1980 when the entire Strait was closed. An extensive monitoring program exists to ensure that only safe shellfish are harvested.

Future prospects — If present trends continue, the Strait of Georgia will come under increasing pressure, particularly from the recreational fishery. Reintroduction of size limits in the recreational fishery along with daily bag limits, area

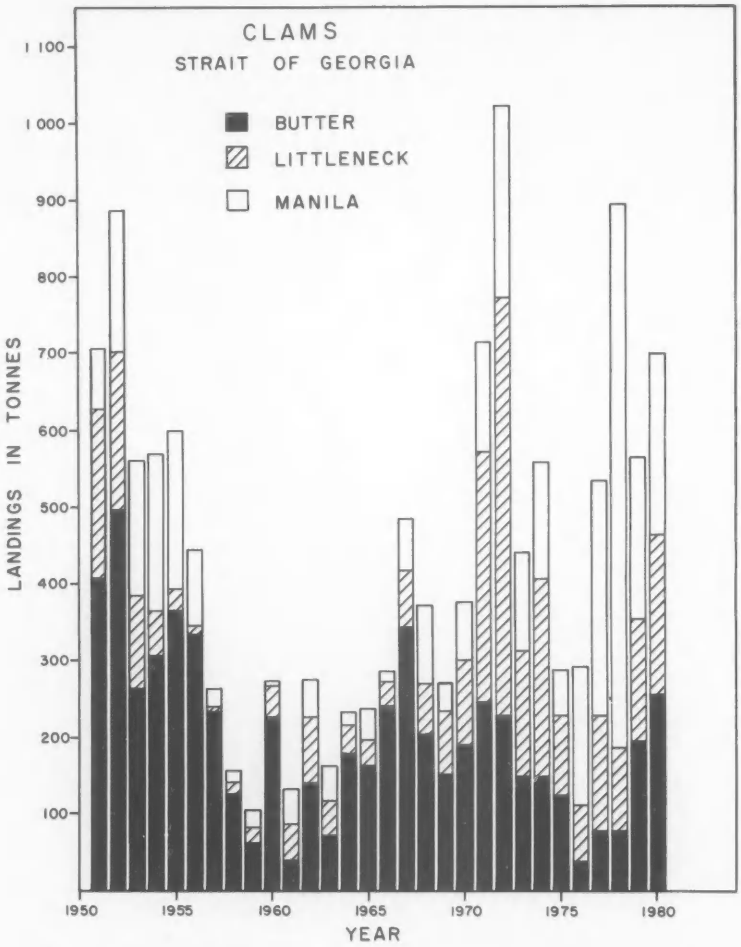

FIG. 13. Canadian production of butter clams, littleneck clams, and Manila clams from the Strait of Georgia (minor statistical areas 13–19).

quotas, and rotational digging may be necessary in management of both the recreational and commercial fisheries. Another way of easing the exploitation pressure would be to encourage increased use of minor species such as soft-shell clams (*Mya arenaria*), cockles (*Clinocardium nuttalli*), blue mussels (*Mytilus edulis*), and horse clams (*T. capax* and *T. nuttalli*).

Several other invertebrate species are used in either or both the commercial and recreational fisheries. A small recreational fishery for abalone (*Haliotis kamtschatkana*) occurs in some parts of the Strait and may come under increasing exploitation. Sporadic and limited commercial fisheries for sea urchins (*Stronglyocentrotus franciscanus*) and sea cucumbers (*Parastichopus californicus*) have occurred in recent years, but the small size of stocks will necessitate stringent management measures. There has also been recent interest in attempts to culture the blue mussel (*M. edulis*), but summer mortalities, fouling, and duck predation will have to be solved before it becomes a large industry. Four species of scallops are occasionally harvested in either or both the commercial and recreational fisheries, but landings are sporadic and small. The weathervane scallop (*Patinopecten caurinus*) exists as a small population in the Gulf Islands area, and because of is value in the restaurant trade, is being considered as a possible candidate for mariculture.

NEW FISHERIES IN THE STRAIT OF GEORGIA

There are three new fisheries in the Strait that deserve

special attention because of their demonstrated or potential economic contribution. One is the commercial fishery for geoducks, a large bivalve that occurs mostly in subtidal waters and is harvested by scuba divers using specialized extraction equipment (Cox 1979). The fishery began in 1976 with landings coming from the east coast of Vancouver Island and grounds near Powell River. By 1979, production had reached 1219 t and, although the catch dropped to 982 t in 1980, it probably will not fluctuate greatly now that quotas have been set for each statistical area within the Strait. Geoducs are sold fresh, frozen, and canned.

The second new and still largely experimental development is a midwater trawl fishery for Pacific hake (*Merluccius productus*). This member of the cod family (Gadidae) exists in the Strait of Georgia as a stock separate from the large migratory stock(s) occurring along the open coast of the United States and southern Canada (Beamish et al. 1982). In winter months, adult hake form large spawning concentrations in midwater (180–260 m) overlying the deep (350 m) central Strait. Discovery of these concentrations along with walleye pollock (*T. chalcogramma*) was made in 1974 (Westrheim 1974), but exploitation did not begin until 1979. Production in both 1979 and 1980 was about 510 t and in 1981 rose to more than 2400 t. Hydroacoustic and ichthyoplankton studies are now in progress to determine abundance and the optimum level of sustainable yield.

The current walleye pollock fishery is pursued mainly with midwater trawl gear in the central Strait area. It qualifies as a new fishery to the extent that the fishing technique and some fishing areas are new, and production was modified by a demand for foodfish (roe and fillets), whereas in the 1950s, the species was used entirely for animal food.

We have little concrete evidence of long-term natural trends in the abundance of pollock in the Strait of Georgia. However, in the Gulf of Alaska, a natural surge in the 1970s has been convincingly documented (Ronholt et a. 1978). Perhaps this has happened in Hecate Strait, where pollock has recently emerged as a major target species (Thompson 1981).

In the absence of direct information, we have to presume that pollock have always been abundant in the Strait of Georgia and that much of the recent surge can be attributed to new market demand and the development of more efficient fishing gear.

Motivated primarily by the market for roe in Japan, production rose from a 1st-yr low of 25 t in 1976 to 1340 t in 1979. Some of the fishing takes place in the open Strait close to the international boundary where there is a contiguous United States fishery of lesser magnitude, 315–580 t in 1979–81, presumably on the same stock of fish (Stocker 1981, p. 39).

Distribution of pollock in spawning condition, as indicated in preliminary studies, suggested there may be more than one stock between Texada Island and the international boundary area (Thompson 1981). Present investigations, however, support the view that the two major concentrations in the Strait between Halibut Bank and the boundary are different age components of the same stock (G. A. McFarlane, personal communication). While a total allowable catch has been applied to the Strait, it is too early to determine the impact of fishing on the stock or its components.

Defunct Fisheries

Halibut — When the Pacific halibut (*Hippoglossus stenolepis*) was still in a primaeval state of abundance in the Northeast Pacific it evidently was of common occurrence in the Strait of Georgia. In the early 1880s, small boats fishing for local consumption caught halibut in English Bay and occasionally even in Burrard Inlet on Vancouver's doorstep (Bell 1981). Thompson and Freeman (1930) reported activities of two fishermen in the Strait in 1888, but no details were given. Probably, Halibut Bank in the central Strait got its name from these early fishermen. Thompson and Freeman also noted activity of other small boat operations at Plumper's Pass close to Victoria, in Puget Sound, and Juan de Fuca Strait. Halibut occurred within Puget Sound as far south as Point-No-Point (Bell 1981).

Today, halibut are a rarity in the Strait of Georgia and if present at all will be found in waters at the eastern end of Juan de Fuca Strait where the link with open waters of the coast is closest. It is unlikely that halibut present before and after the turn of the century were no more than seasonal visitors or strays. The species appears to require open coast conditions like those along the continental slope where spawning occurs in 200–460 m and larvae are free to drift for hundreds of miles to rearing areas in the colder waters of the Gulf of Alaska and Bering Sea (Anonymous 1978). Although there are a few spawning grounds off the British Columbia coast there are no known rearing areas for young juveniles (0–3 yr).

Whales — It is evident from early reports that humpback whales (*Megaptera novaeangliae*) were seasonal (summer) visitors to the Strait of Georgia. There must have been considerable numbers because at least two attempts were made to set up whaling stations within the Strait.

First reports, as indicated by file records held at the Maritime Museum in Victoria, state that whaling commenced in 1868 out of Whaletown on Cortez Island at the northern end of the Strait (M. Bigg, personal communication). Two years later, the operation was moved to a more strategic location in the Strait, in what is now known as Whaling Station Bay on Hornby Island. By late 1871, catches were reported as getting smaller and scarce, and by 1872, the company went bankrupt (Langevin 1872).

The second attempt was not made until around 1907 when a fully equipped station was installed at Page's (commonly Piper's) Lagoon near Nanaimo on Vancouver Island (Taylor 1907). Whales must have been in short supply because during 1907–08 the station had to resort to processing landings of dogfish, which were reduced to fertilizer. By 1908–09, the station had been dismantled for lack of whales and the equipment was transferred to the west coast of Vancouver Island (Taylor 1909).

In none of the early accounts is there any reference to the numbers of whales processed in a stated period. Indeed, it is apparent that at least one company would not provide information to government officials (Anderson 1872).

During the late 1800s and early part of the present century, whaling stations were active at several localities along the outer coast of British Columbia, and reports suggest that whales were in high abundance. Possibly, those humpbacks

that seasonally entered the Strait of Georgia did so initially as strays or "overflow" from areas along the exposed coast. Eventually, through a learning process passed from generation to generation, a local stock emerged that returned year after year to the Strait. In fact, individuals are known to return to the same inshore inlets each year in Southeast Alaska. Under such conditions, once a local stock is eliminated by hunting, it would take many years for a new stock to emerge, particularly if the offshore stock(s) from which it originated had been greatly reduced in size. Although land-based whaling along the British Columbia coast ceased in 1968 and pelagic whaling is now greatly reduced, the total population of humpbacks in the eastern North Pacific is still very low and probably explains their scarcity in the Strait of Georgia (M. Bigg, personal communication).

A small live-capture "fishery" for killer whales (*Orcinus orca*) occurred in British Columbia and Washington during 1962–77 to supply oceanaria (Bigg and Wolman 1975; Bigg 1982). This enterprise is now tightly controlled and further recaptures are allowed only for Canadian aquaria to replace whales that have died. Killer whales that occur in the Strait of Georgia are part of a southern community consisting of three pods, one of which is confined to the Strait and Puget Sound. The other two occupy the same inshore waters but have a wider range that includes Juan de Fuca Strait and areas off the west coast of Vancouver Island and Washington. In all, about 80 whales are involved (Bigg 1982).

Harbor seals — From at least as early as 1914, the harbor seal (*Phoca vitulina*) was the object of a "fishery" in the sense that it was hunted for a bounty paid by the Canadian Department of Fisheries. This practice continued until 1964 (Biggs 1969). From 1963 to 1969, it was hunted for its pelt, and during the peak year (1965), a total of 873 animals were killed in the Canadian portion of the Strait of Georgia alone. From 1970 to the present, hunting of the harbor seal has been banned completely.

It is likely that the population of seals in the Strait has increased during the past decade and, as noted earlier, may be a factor in the currently low abundance of lingcod. The Steller's sealion (*Eumelopias jubatus*) and recently arrived California sealion (*Zalophus californianus*) in the Strait of Georgia are also on the protected list and are increasing in abundance. They are likewise suspects as predators on lingcod.

Discussion and Summary

The fishery future of the Strait of Georgia will depend to some extent on long-term policy decisions regarding the coexistence of commercial and recreational fisheries and on the success of measures to control environmental degradation by domestic and industrial pollution. We have cited instances where recreational fisheries are expected to take an increasing share of some resources, perhaps to the point of displacing commercial operations. Pollution is already limiting utilization of some resources (e.g. clams) and may be having a detrimental effect on others.

The Strait of Georgia is by no means a simple self-contained system. However, to biological oceanographers it presents some advantages not the least of which is the logistical convenience of the area and the prospect that, given sufficient funds, monitoring systems could be established to measure man-made changes in the environment, as well as to detect major natural events that might provide forecasts of value to fishery managers. Yet, amongst the fisheries and stocks we have examined (albeit superficially), the dynamics of relatively few seem to be clearly and predominantly influenced by natural events in the Strait. The most outstanding example is that of the Pacific oyster whose irregular but massive fluctuations in spatfall are dependent on warm summers when surface temperatures are high enough. There are indications that some herring year-classes are favored by cold winters. Productivity of the Dungeness crab also appears to be associated with warm springs and summers, not only in the year of capture but at time of spawning.

While economic factors appear to guide the fortunes of clam resources, along with some indications of overfishing, fluctuations in production at times are intimately tied to the intensity and distribution of "red tide" (*Gonyaulax*) blooms. Thus far, these have been impossible to predict or to avoid.

Fluctuations both long- and short-term that have been observed in Pacific cod abundance may have some connection with environmental factors but more likely reflect an intrinsically biological phenomenon, a density-dependent rate of natural mortality, as suggested by D. Fournier (unpublished data) for cod in another region of the coast.

We have observed long-term declines in the catch of flatfishes in general and in the index of abundance of English sole in particular. These may be the result of overfishing but could reflect environmental degradation in intertidal waters. Similar uncertainties attend the cause of declining abundance of lingcod and some species of shrimp.

Theoretically, answers should not be hard to obtain, but questions of overfishing, environmental degradation, intraspecific compeition, fluctuations in predator stocks (dogfish, seals, and sealions), etc., cannot be answered with the low level of support that perforce is allotted for investigation of inshore fisheries.

As one way of summarizing this review it is instructive to pull the various fisheries of the Strait of Georgia together to examine their current commercial worth. The total landing in 1980 was almost 25 000 t having a landed value of 20 million dollars and a marketed value of about 104 million dollars (Table 1) (Anonymous 1980). In relation to the British Columbia coast as a whole, the contribution of the Strait of Georgia was 27% by weight, 34% by landed value, and 26% by wholesale value.

Herring overshadowed all other species, accounting for 58% of the landing and 71 and 90% of the landed and wholesale values, respectively. This leaves nearly 10 500 t of fish and shellfish that, more so than herring, can be called full-time residents of the Strait of Georgia. In 1980, the landed value was almost 6 million dollars and the wholesale value 10 million dollars. These are minimum estimates, since landings of some species are not recorded on sales slips or are sold directly to the public.

To complete the picture, we should include the recreational fishery for such species as lingcod, crabs, shrimps, prawns, clams, and oysters. However, this is doubly difficult, since

TABLE 1. Landed weight, landed value, and wholesale value of species contributing to the 1980 marine fisheries of the Strait of Georgia (weights in tonnes and values in thousands of dollars).

Species	Landed weight	%	Landed value	%	Wholesale value	%
Herring[a]						
Bait and foodfish	5 350		3 538		4 371[b]	
		57.9		70.7		90.3
Roe	9 070		10 730		89 836[b]	
Dogfish	2 108	8.5	391	1.9	1 108	1.1
Pacific cod	1 623	6.5	804	4.0	1 680	1.6
Pollock	1 056	4.2	211	1.0	890	0.9
Hake	508	2.0	61[c]	0.3	(183)[d]	0.2
Lingcod	423	1.7	347	1.7	699	0.7
English sole	114	0.6	48	0.2	24	*
Other flatfish	245	1.0	114	0.6	399	0.4
Other groundfish[c]	238	1.0	106	0.5	102	0.1
Dungeness crab	411	1.7	717	3.6	638	0.6
Shrimps	145	0.6	598	3.0	869	0.8
Oysters	1 798	7.2	1 134	5.6	1 274	1.2
Geoducks	982	3.9	808	4.0	1 254	1.2
Butter clams	255	1.0	85	0.4	323	0.3
Littleneck clams	210	0.8	181	0.9	313	0.3
Other clams	335	1.3	256	1.3	335	0.3
Other invertebrates[e]	27	0.1	52	0.3	86	0.1
Total	24 898	100.0	20 181	100.0	104 304	100.0

[a]Fishing season November 1980–March 1981. Hailed weights.
[b]Estimated on the basis of ratio of landed to wholesale value in the preceding 1979–80 season.
[c]Includes rockfish species, sablefish, skate, perch.
[d]Catch processed at sea. Landed and wholesale values are estimated on the basis of 1981 fishery, which included landed catches.
[e]Includes squid, octopus, sea urchins.

not only are the estimates of catch unreliable, but we run into the snarl of attempting to attach a monetary value to the recreational fishery. No such attempt can be made here.

In looking to the future, we must presume that the recreational share of the fish and shellfish resources of the Strait of Georgia is going to expand with increasing population. We must also presume that as the share increases, pressure from recreationists on legislators and managers will become appreciably greater. Thus, there are difficult questions about the future of the commercial fishery for herring, which is already being managed on the conservative side, as much to prevent recurrence of the disastrous collapse of the late 1960s as to ease the pressure from sportsmen who mistakenly presume that the more herring there are, the better the growth and survival of chinook and coho salmon (see Healey's 1976 assessment of this issue).

Increased spearfishing as a sport, if it has not already had impact on inshore commercial fishing for lingcod, is likely to increase. Some clam beaches are already being harvested at too high a level as the result of expanded recreational activity and the same may befall the fisheries for crabs, prawns, and shrimps. Although the Pacific cod is not fished recreationally to any significant degree in the Strait, this may just be a matter of time, as it is already a popular activity in Puget Sound.

It is difficult to imagine that sports fishermen will ever be serious competitors with the commercial enterprise on dogfish. Most sportsment (and most commercial fisherman not dependent on dogfish for a living) would prefer to see the species reduced to a fraction of its present abundance either by commercial fishing or some government funded program of "pest control."

Recreational fishing for hake, pollock, and most flatfishes is unlikely to assume significant proportions because of access problems and the need for specialized gear. The subtidal geoduck probably fits in this category too.

We foresee greater recreational use of several species of smelts (the capelin, *Mallotus villosus*, and surf smelt, *Hypomesus pretiosus pretiosus*), which though highly seasonal in their appearance are accessible along many beaches bordering the Strait. The anadromous eulachon (*Thaelichthys pacificus*), which lives in the Strait of Georgia and spawns in the lower reaches of the Fraser River, likely will continue to be of commercial interest only, because of the difficulty of access. Within the Strait there are numerous species of rockfish (*Sebastes*) commonly called rockcod that until recently were little used by the commercial fisheries because of economic conditions (the 1980 landing was only 40 t). The copper rockfish (*Sebastes caurinus*) and the quillback rockfish (*Sebastes maliger*) are two shallow-water species that are readily available to jigging gear on rocky bottom. Others such as the yelloweye rockfish (*Sebastes ruberrimus*), or red snapper as it is more commonly called, are to be found in deeper waters.

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Review of the Benthos of the Strait of Georgia and Contiguous Fjords[1]

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The distribution of benthic communities in the Strait of Georgia is partially determined by the relative areas of various sediment types, their depths, and characteristics of overlying water. Rocky shores, which account for 88% of the shoreline length, have been fairly closely examined and communities have been described in the context of worldwide zonation patterns. The ecology of macrofauna and meiofauna of unconsolidated sediments at several estuaries (Nanaimo, Fraser, Squamish) has been documented. In eelgrass beds, very diverse invertebrate communities are found, whereas in brackish marshes closer to river mouths the ecosystem is characterized by a few very abundant species. To date, between 325 and 350 macroalgae species have been recorded from the shallow subtidal habitats of the Strait. In an intensive study at Bath Island, 10 algal communities were defined, each with an associated faunal group. The deep subtidal habitats are extensive: 71% of the surface area of the bottom of the Strait is between 50 and 300 m. These habitats are dominated by burrowing macrofauna such as holothurians, bivalves, and the heart urchin, *Brisaster latifrons*. The fauna of the rocky walls of fjords connecting with the Strait are characterized by cup corals, brachiopods, and sponges. Even though subject to low and fluctuating dissolved oxygen levels, a diverse fauna of epilithic organisms has been found in Saanich Inlet. Agglomeration, flocculation, and zooplankton pelletization are important mechanisms for transport of phytodetrital food for deep subtidal benthos. Provision of organic material from nearshore and riverine production sites is very important because of the extensive shoreline around the Strait. Juvenile salmonids, especially chinook (*Oncorhynchus tshawytscha*) and chum (*O. keta*), are strongly shoreline oriented and feed on epibenthic crustaceans and insects on foreshores. The deeper subtidal habitats in the Strait apparently do not support productive bottom fish communities. Although the major benthic assemblages have been described and standing crops have been estimated, there are very few data on the dynamics of benthic communities, secondary production of zoobenthos, benthic–pelagic coupling, or the quantitative relationships between oceanographic variables and benthic production.

LEVINGS, C. D., R. E. FOREMAN, AND V. J. TUNNICLIFFE. 1983. Review of the benthos of the Strait of Georgia and contiguous fjords. Can. J. Fish. Aquat. Sci. 40: 1120–1141.

La distribution des communautés benthiques du détroit de Géorgie est partiellement déterminée par la superficie relative des divers types de sédiments, leurs profondeurs et les caractéristiques des eaux sus-jacentes. Les rivages rocheux, qui constituent 88 % de la longueur de la ligne de rivage, ont été examinés d'assez près et les communautés décrites dans un contexte de zonation à échelle globale. On a étudié l'écologie des macro et méiofaunes des sédiments non consolidés de plusieurs estuaires (Nanaïmo, Fraser, Squamish). On trouve dans les lits de zostère marine des communautés d'invertébrés très diverses, alors que, dans les marais d'eau saumâtre situés plus près de l'embouchure des rivières, l'écosystème est

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caractérisé par quelques espèces très abondantes. À ce jour, on a signalé entre 325 et 350 espèces de macro-algues dans les habitats subtidaux peu profonds du Détroit. Au cours d'une étude intensive menée à l'île Bath, on a défini 10 communautés algales, chacune contenant un groupe faunique associé. Les habitats subtidaux profonds sont étendus: 71 % de la superficie du fond du Détroit sont compris entre 50 et 300 m de profondeur. Ces habitats sont dominés par une macrofaune fouisseuse, telle que holothuries, bivalves et spatangues (*Brisaster latifrons*). La faune des parois rocheuses des fjords débouchant sur le Détroit est caractérisée par des caryophyllies, brachiopodes et éponges. Dans l'inlet Saanich, bien qu'il soit sujet à des niveaux d'oxygène dissous faibles et variables, on a trouvé une faune diverse d'organismes épilithiques. Le transport d'aliments phytodétritiques pour le benthos subtidal des profondeurs est assuré surtout par des mécanismes d'agglomération, de floculation et de réduction du zooplancton en boulettes. À cause d'une ligne de rivage étendue autour du Détroit, les apports de matières organiques des sites de production côtiers et fluviaux sont très importants. Les jeunes salmonidés, surtout saumons chinook (*Oncorhynchus tshawytscha*) et keta (*O. keta*) sont très orientés vers la côte et se nourrissent de crustacés et d'insectes épibenthiques dans les avant-plages. Il semble que les habitats subtidaux du Détroit ne supportent pas de communautés productives de poissons démersaux. Bien que les principaux groupements benthiques aient été décrits et les biomasses estimées, il n'existe que très peu de données sur la dynamique des communautés benthiques, la production secondaire de zoobenthos, la liaison benthique–pélagique ou les relations quantitatives entre variables océanographiques et production benthique.

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THE benthic communities of the Strait of Georgia have become of interest, particularly because of increasing pressure from human infringement. Impacts of ocean dumping, industrial pollution, shipping, marine harvesting, and dredging need determining, but there are also a number of problems intriguing to basic research. By virtue of its extensive shoreline length, estuarine character, areas of turbulent mixing, high primary production, and oxygen deficient environments in contiguous fjords, a host of oceanographic problems relating to benthic ecology can be identified.

Our objective was to present an overview of benthic community structure in major habitats and to discuss possible links to oceanographic features, to generally describe production processes, and to summarize the existing literature on the importance of benthic production to fish food webs. The proliferation of multidisciplinary studies in modern oceanography testifies to the acknowledgment of the importance of physical and chemical features in the development of biotic assemblages. An ecosystem analysis is not possible without frequent reference to independent and extrinsic variables of the environment. Unfortunately, there are few such systems approaches in the benthic work of the Strait: studies of the benthos here are mostly still in the descriptive phases.

Geological and Oceanographic Setting

Detailed information on the Strait of Georgia is available for both its geological (Luternauer et al. 1983) and physical oceanographic (Thomson 1981; LeBlond 1983) characteristics. The major physiographic features, water bodies, and specific locations mentioned in this paper are shown in Fig. 1. Romaine et al. (1981) have provided folios documenting shoreline type from Campbell River to Cowichan Bay on the east coast of Vancouver Island. The authors provided coincident biological resource information with geological data. We have computed the lengths and areas of the various substrates and depths using designations on hydrographic charts. Information on bottom type was sufficiently detailed only for intertidal and subtidal habitats down to 20 m (Table 1). Rocky and sandy shores predominate, accounting for 88.0% of the total 3721 km of shoreline in the Strait and contiguous inlets. When area is considered, however, sand and mud substrates are more extensive, representing 66.8% (832 km^2) of the total 1245 km^2 of intertidal and subtidal habitats. Rocky shores only contribute 320 km^2 or 25.7%.

Areas at depths >20 m in the main part of the Strait, Saanich Inlet, and Howe Sound were computed from Natural Resource Maps Nos. 15783-A, 15792-A, 15794-A, and 19304-A published by the Geological Survey of Canada. The data are as follows:

Depth zone (m)	Area (km^2)	%
20–50	800	10.8
50–100	1560	21.1
100–200	2130	28.8
200–300	1570	21.2
300–400	1000	13.5
>400	330	4.5
Total	7390	

Seventy-one percent of the area is accounted for by the 50- to 300-m depth range.

The oceanographic features of the surface waters of the Strait are highly variable, reflecting the influence of topography, river runoff, tides, and winds. Except in passages where tidal mixing is very strong or circumstances in shallow waters where heavy wave action is encountered, shallower depths are almost always characterized by lower salinity

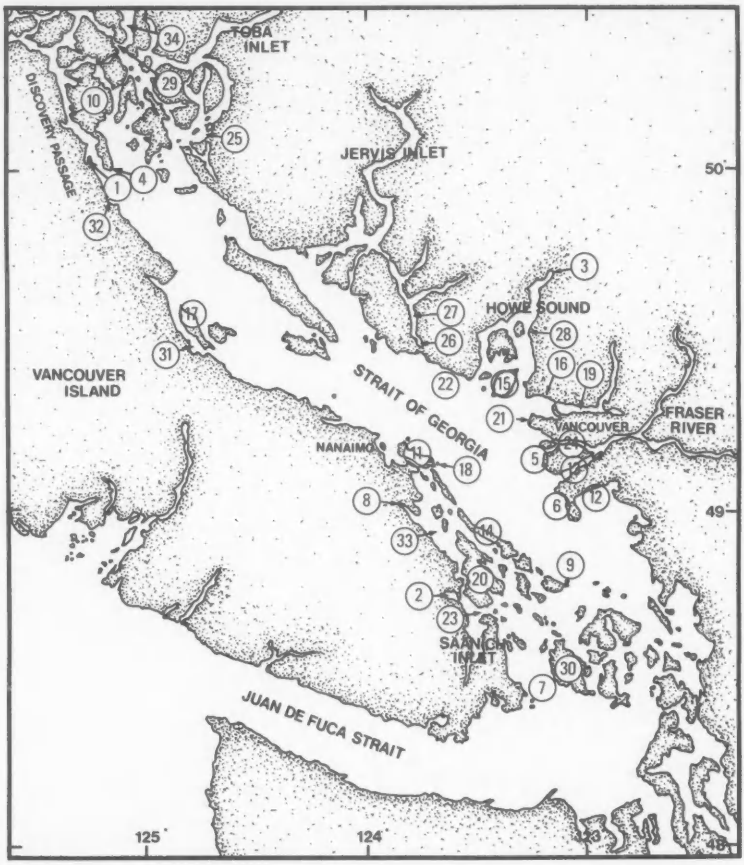

FIG. 1. Major physiographic features of the Strait of Georgia and locations of specific sites mentioned in the text. Key to numbered locations is as follows: 1, Campbell River, Campbell River Estuary; 2, Cowichan Bay, Cowichan River Estuary; 3, Squamish River Estuary; 4, Cape Mudge; 5, Sturgeon Bank; 6, Roberts Bank; 7, Haro Strait; 8, Ladysmith Harbour; 9, East Point; 10, Seymour Narrows; 11, Gabriola Island; 12, Boundary Bay; 13, South Arm of Fraser River; 14, Galiano Island; 15, Bowen Island; 16, West Vancouver; 17, Denman Island; 18, Bath Island; 19, Burrard Inlet; 20, Saltspring Island; 21, Point Grey; 22, Halibut Bank; 23, Satellite Channel; 24, North Arm of Fraser River; 25, Prideaux Haven; 26, Porpoise Bay; 27, Sechelet Inlet; 28, Porteau; 29, Yuculta Narrows; 30, San Juan Island; 31, Baynes Sound; 32, Oyster River; 33, Stuart Channel; 34, entrance to Bute Inlet and Homathko Estuary.

compared with deeper samples. Therefore, almost all of the water in the Strait is stratified, imparting an estuarine character to the whole water body.

Locations close to river mouths are perhaps the most variable sites, where annual surface salinities can range from 0‰ up to approximately 28‰ depending on river stage. These ranges were measured near the mouth of the Squamish River (Levings and Moody 1976), which is a river characterized by two major runoff periods, an early summer runoff due to ice and snow melt and an autumn freshet resulting from heavy fall rains. Local freshening at locations where rivers are not fed by snowmelt tends to occur in autumn–winter only. Where river channel depth is sufficient, a salt wedge migrates into estuaries at high tide and low runoff. In the lower Fraser, for example, surface waters can be completely fresh, while bottom water at 10 m is characterized by water of up to 25‰ (Hughes and Ages 1975).

Stations along the longitudinal axis of the Strait show the pervading influence of the Fraser River on surface salinities, and locales at the northern end show a narrower range of surface salinities than do those closer to the river mouth. For example, Cape Mudge experiences a seasonal mean range of

TABLE 1. Estimates of length and area of six shoreline types of the Strait of Georgia and adjacent inlets (excluding Burrard Inlet). Angles indicate assumed slope to 20 m depth. Data from chart symbols; scale of chart used 1:153 734 (from Foreman 1976b).

Substrate type	Shoreline length (km)	Area (km^2)
Rocky shores, steep (60°)	1357	54
Rocky shores, gentle (45°)	1063	266
Gravel (25°)	248	93
Sand (10°)	849	424
Mud (5°)	204	408
Total	3721	1245

27.1−29.1‰ (Hollister and Sandnes 1972) compared with 0−25‰ for Sturgeon Bank (Conlin et al. 1982).

Surface water temperatures in the Strait are influenced by seasonal warming, tidal mixing, and by river runoff. Glacier-fed rivers such as the Squamish and Homathko impart a low-temperature regime on their estuaries. The seasonal range of inshore surface waters at Squamish is approximately 4−12°C (Levings and Moody 1976) compared with 6.2−17.6°C at Departure Bay, near Nanaimo (Hollister and Sandnes 1972), which is probably representative of the west coast of the Strait. Seasonal heating is more pronounced at localities where river runoff is reduced and tidal currents are minimal, for example at Ladysmith Harbour where the seasonal range is 5.5−20.6°C. Probably the coolest nonestuarine locations are the passes and channels where tidal mixing reduces any stratification effects and/or where the influx of cooler oceanic water might be expected. For example, surface temperatures at East Point range from 7.1 to 11.6°C (Hollister and Sandnes 1972).

Tides in the Strait of Georgia are of the mixed, semidiurnal type. Effects of narrowed topography in fjords, atmospheric pressure, and river runoff all influence local tide levels. River runoff is particularly important in the lower Fraser River. According to standard tide books, a maximum range of 5.55 m would be expected at Prideaux Haven, at the north end of the Strait. The minimum range, 2.96 m, would be expected at Porpoise Bay, at the south end of Sechelet Inlet. At locations on the open Strait the usual amplitude for large tides is about 4.80 m.

Tidal current speeds in the passes connecting the main body of the Strait with inlets and broader channels are extremely swift, among the highest in the world oceans according to some authorities. In Seymour Narrows, surface currents up to 700 $cm \cdot s^{-1}$ or greater are usual on spring tides. Currents at freshet near the mouth of major rivers such as the Fraser, Squamish, and Homathko are in this range, also, especially on ebbing tides. Surface currents around the shorelines in the main body of the Strait are more passive (Thomson 1981).

In contrast with the variable nature of the surface waters the available recent temperature, salinity, and dissolved oxygen data (Crean and Ages 1971) showed the deep basins to be among the most stable benthic environments in the Strait. Temperature at 50 m ranged from 10°C in July to 7°C in January, with little evidence of variation with latitude. At 100 m and deeper there was less seasonal change, with a range of 8.5−9.0°C. The salinity range at 50 m was 29.0−30.0‰ at the shallow depth, narrowing to 30.5−31.0‰ at 100 m and deeper. Seasonal range of dissolved oxygen here is from 3.0 to 4.0 $mL \cdot L^{-1}$. Bottom currents tend to be low and predictable (e.g. Waldichuk 1957) although there is evidence of stronger current on the Fraser Delta slope (Luternauer et al. 1983). In general, properties of the bottom waters of the Strait fluctuate seasonally, within the ranges given above, responding to the pulses of oceanic water penetrating through Juan de Fuca and Haro straits (Thomson 1981). Because of the intense tidal mixing through the channels and passes, there is usually very little stratification of properties, as is observed in the major basins of the Strait (Herlinveaux and Giovando 1969). Relatively shallow channels such as Discovery Passage show seasonal changes of a minor nature, varying from 29.0 to 30.5‰ at depths >20 m in 1959−60. Deeper passes such as Haro Strait show evidence of intrusion of higher salinity water from the Strait of Juan de Fuca, so that at 200 m seasonal range in salinity was 30.5−32.5‰. At both passes there is little evidence of seasonal warming at depth (7.0−8.5°C); dissolved oxygen usually exceeded 5.6 $mL \cdot L^{-1}$. As mentioned, currents here can be very high. Below 100 m in Stuart Channel (July, 1959) salinity values were in the range 29.5−29.8‰, temperatures were 9.1−9.5°C, and dissolved oxygen values ranged from 1.5 to 2.8 $mL \cdot L^{-1}$ (Waldichuk 1964). The latter data were not influenced by pulpmill effluent, as effects were restricted to upper layers.

Three of the fjords of this area that are confluent with the Strait of Georgia have been studied. Jervis Inlet is the longest and deepest (680 m); it and Howe Sound (285 m deep) are on the eastern side of the Strait whereas Saanich Inlet (230 m maximum depth) is on southern Vancouver Island (Fig. 1). The mouth of Jervis is unrestricted but the outer region of Howe Sound is separated from the main strait by a sill that rises to 45 m from the surface. A similar sill is present at Saanich Inlet but at the mouth where it rises to 70 m.

Temperature and salinity characteristics in these fjords do not vary greatly from those of the adjacent Strait although freshwater runoff may affect local waters. Oxygen levels in Jervis Inlet have been measured in mid-depth as low as 2.0 $mL \cdot L^{-1}$ (Lazier 1963), but such values are infrequent. The sills of Howe and Saanich, however, interfere with deep-water exchange. The deep waters of the inner area of Howe Sound may fall below 1.0 $mL \cdot L^{-1}$ (Bell 1973; Levings 1980a), while those of Saanich frequently are anoxic (Richards 1965; Anderson and Devol 1973). Both inlets are

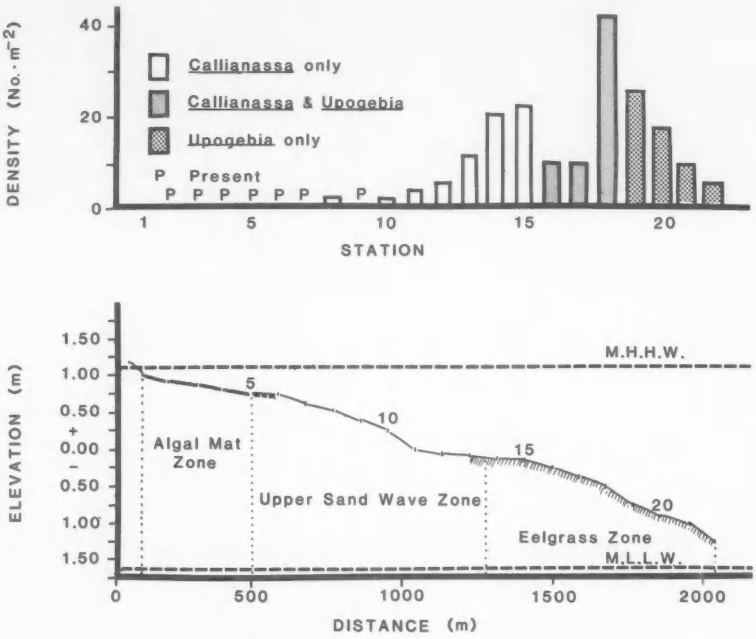

FIG. 2. Abundance of two thalassinidean shrimp, *Callianassa californiensis* and *Upogebia pugettensis*, on a transect through the intertidal zone on Boundary Bay (from Swinbanks and Murray 1981).

subject to annual deepwater renewal.

Further oceanographic observations on these fjords have been made by Carter (1934), Pickard (1961), Pickard and Stanton (1980), Waldichuk et al. (1968), Fulton et al. (1969a), Herlinveaux (1962), Bell (1973, 1975), and Coastal Zone Oceanography Section (1980).

Benthic Communities

Studies of the benthic biota of the Strait of Georgia began in the late 1800's, when the dominant fauna were first to be described. Early investigators, such as Taylor (1895) who sampled molluscs and Berkeley (1923) who worked on polychaetes, concentrated on the intertidal zone and shallow subtidal areas. Most early taxonomic publications are referenced elsewhere, especially in Bernard et al. (1967), Marles (1973), and Austin and Deutsch (1978). McLean-Fraser (1932) provided an early synthesis of the available faunal data, in this case for a comparison with Puget Sound information. The earliest major collection of benthic algae in the Strait was by Collins (1913). Connell (1928) collected algae in the vicinity of Departure Bay. Following World War II, Dr R. F. Scagel and his students compiled an extensive collection of algae now housed at the University of British Columbia Herbarium, including an extensive collection around Gabriola Island by South in 1966–67. These collections are summarized by Foreman and Root (1975). Surveys or studies that have added to our knowledge of benthic communities in the Strait have been more frequent and comprehensive since about 1960. These later studies form the basis for the following descriptions of communities and habitats, which have somewhat arbitrarily been designated on the basis of substrate type, depth, and oceanographic features. Most of the major habitats have now been covered, albeit with varying intensity.

Intertidal Habitats

The biota on tidal shores of the Strait of Georgia were the first to be investigated by natural historians and marine biologists. Until recently, emphasis has been on rocky shores, but since about 1970 there have been several concerted efforts to understand soft sediment intertidal habitats. It is convenient to review the published work using sediment type as a classification guide as did Bousfield (1957) in one of the earlier descriptions of the Strait fauna. In addition, because of the importance of vegetation in determining faunal composition, animals using eelgrass beds and brackish marshes are discussed. In many embayments and beaches, there is often a mosaic of sand, mud, and vegetation, but the following review deals with large areas where there is homogeneous substrate or vegetation greater than about 1 km^2.

Sand beaches — Studies of sandflat organisms have been conducted in Boundary Bay and on Roberts Bank, Fraser River Estuary. Kellerhalls and Murray (1969) were the first to report on macrobenthos of sand at Boundary Bay. More detailed studies were reported by Swinbanks (1979),

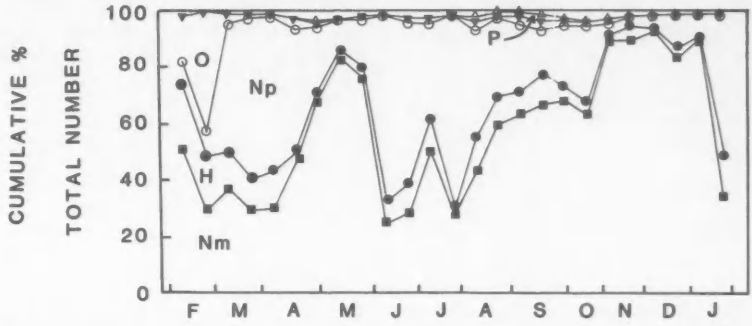

FIG. 3. Seasonal changes in major groups of meiobenthos in sandflats on northern Sturgeon Bank, Fraser River Estuary (from Harrison 1981). P, polychaetes; O, oligochaetes; Np, nauplii; H, harpacticoids; Nm, nematodes.

Swinbanks and Murray (1981), and Smith (1981). Swinbanks and Murray's "upper sand wave zone" (Fig. 2) was between 0 and 0.75 m (geodetic), and sediments had a mean grain size in the range 3.1−2.7 mm with <1% mud content. Macrofauna studied by Swinbanks and Murray (1981) included polychaetes *Abarenicola pacifica* and *Spio* sp., the decapods *Callianassa californiensis* and *Upogebia pugettensis*, the bivalve *Mya arenaria*, and the gastropod *Batillaria attramentaria*. These were the dominant species in the upper sand wave zone and the eelgrass zone, located below the former area. Dominant fauna in the "lower sand wave zone," near tidal datum, were the sand dollar *Dendraster exocentricus* and the polychaetes *Clymenella torquata* and *Abarenicola* sp. The burrow structures, sediment traces, and sediment turnover were documented by the authors, as well as potential causes for zonation of biota. Swinbanks (1979) estimated that *A. pacifica* of Boundary Bay reworked about 10 Mm^3 of sand per year. Boundary Bay was a particularly useful area to study zonation on a soft sediment shore, as there is very little change in sediment grain size on an extensive beach with an elevation change of >3.0 m.

Swinbanks (1979) also investigated sandy shores on Roberts Bank. At this part of the Fraser Estuary, salinities are lower and mud content of sediments is higher because of proximity to the mouth of the river. *Upogebia pugettensis* were localized on southern Roberts Bank and were correlated with mud content; *C. californiensis* abundance decreased markedly on northern Robert Banks close to the South Arm of the Fraser.

The smaller macrofauna (animals retained on a 0.5-mm sieve) have also been examined on the sand flats of Roberts and Sturgeon banks. Levings and Coustalin (1975) found that densities of the bivalve *Macoma balthica* decreased seaward on several long transects. Crustaceans such as the tube-building amphipod *Corophium salmonis* also were less abundant in sand sediment farther offshore. Spionid polychaetes such as *Pygospio elegans* were able to use the sandflats at some localities. The haustoriid amphipod *Eohaustorius washingtonianus* was the most abundant crustacean in the well-sorted sand at the lower part of the transects.

Harrison (1981) conducted a comprehensive study of harpacticoid copepod (meiofauna) ecology on the sandflat on northern Sturgeon Bank. Among the topics studied were seasonal variations (Fig. 3), interspecific competition and community structure, and spatial pattern with respect to sediment type on the scale of centimetres. Detailed autecological research on eight taxa, namely *Scottolana canadensis*, *Halectinosoma* sp., *Pseudobradya* sp., *Tachidius triangularis*, *Leptastacus constrictus*, *Paraleptastacus spinicauda*, *Huntemannia jadensis*, and *Limnocletodes behningi*, was conducted. Data were also provided on seasonal change in redox potential, salinity, and dissolved oxygen within the sediment.

Rocky shores — As noted by McLean-Fraser (1932) and Bousfield (1957) there is considerable variation in the slope and geology of the rocky shores around the Strait, with corresponding biological changes. On Galiano Island, for example, flattened benches of sandstone have been eroded into tide pools. In contrast, the granitic shoreline of Bowen Island drops almost vertically into the sea. These geological factors, in association with water characteristics, wave energy, and biological interactions, are thought to be the major agents influencing faunal composition at specific sites. The biology of rocky shore fauna recorded from the Strait was described by Ricketts and Calvin (1968), Carefoot (1977), and Lewis and Quayle (1972). Representatives of almost all phyla were listed in an early survey (1936) of the shores of Coffin Island, near the entrance to Ladysmith Harbour (Quayle 1970).

Intertidal biota were quantitatively sampled and described by R. E. Foreman and associates as part of a 6-yr nearshore benthic ecology study of the Strait of Georgia (see section on subtidal habitats less than 20 m). Nassichuk (1975) experimentally investigated the relationships between *Fucus* structure and associated intertidal fauna on Bowen Island, obtaining a positive correlation between structure and faunal diversity. Wu and Levings (1979) provided a brief description of fauna associated with barnacles (*Balanus glandula*) on rocky shores at West Vancouver. In addition, there are numerous papers dealing with the biology of species found in the Strait but studied elsewhere, for example in Puget Sound (see Ricketts and Calvin 1968), but surprisingly few local data.

In 1947, Stephenson and Stephenson (1961a, 1961b) examined the shore biota of Brandon Island, Departure Bay, as part of their worldwide studies into the causes of intertidal zonation. Differences in fauna between the north and south sides of Brandon Island were documented. Invertebrates that dominated communities in each of the "zones" were as follows:

Supralittoral fringe	Midlittoral zone	Infralittoral fringe
Littorina scutulata[a]	*Chthamalus dalli*[c]	*Pisaster ochraceus*[f]
Ligia pallasi[b]	*Balanus glandula*[c]	*Pisaster brevispinus*[f]
	Balanus crenatus[c]	*Dermasterias imbricata*[f]
	Balanus cariosus[c]	*Evasterias troschelli*[f]
	Acmaea pelta[a]	*Pycnopodia helianthoides*[f]
	Acmaea persona[a]	*Serpula vermicularis*[g]
	Littorina sitkana[a]	*Diodora aspera*[a]
	Mytilus edulis[d]	
	Crassostrea gigas[e]	

[a]Mollusca–Gastropoda.
[b]Crustacea–Isopoda.
[c]Crustacea–Cirripedia.
[d]Mollusca–Bivalvia.
[e]Mollusca–Bivalvia; not present in 1947 but dominant in 1960.
[f]Echinodermata–Asteroidea.
[g]Polychaeta–Sedentaria.

Stephenson and Stephenson (1961a, 1961b) also examined rocky shores on Horswell Bluff, an exposed site on the north side of the entrance to Departure Bay and at a reef in tide-swept False Narrows, between Gabriola and Vancouver islands. Differences in fauna at the latter two locations in comparison with Brandon Island were attributed to major changes in algal communities, substrate composition, and wave and current energy.

Mud flats — The most extensive mudflats in the Strait of Georgia are at the Fraser Estuary. Inshore of Sturgeon and Roberts banks a band of fine sediment, up to 2 km wide, is found immediately seaward of the brackish marshes outside the sea dykes. There are smaller areas of mud in other estuaries, since it is the finer material brought down by rivers that provides the source sediment for these habitats. Examples where data on fauna are available include the Squamish Estuary (Levings 1980b) and Maplewood mudflats in Vancouver Harbour (Levings and McDaniel 1974).

Characteristic macrobenthic organisms in the mudflats of the Fraser Estuary are the bivalve molluscs *Macoma balthica* and *Mya arenaria*, the polychaetes *Manayunkia aestaurina*, *Hobsonia florida*, *Nereis* (*Neanthes*) *limnicola*, and *Pygospio elegans*, and the amphipod *Corophium salmonis* (Levings and Coustalin 1975; Otte and Levings 1975). Using a 0.8-mm sieve, total faunal abundance ranged up to 8500 individuals $\cdot m^{-2}$ and 144 g wet wt $\cdot m^{-2}$ on Sturgeon Bank. McGreer (1979) sampled *M. balthica* on the mudflats near Brunswick Point, Roberts Bank, between April 1977 and March 1978 with 0.5-mm sieves. Density reached a peak of 1817 individuals $\cdot m^{-2}$ in late April, about the same time as maximum biomass (6.3–7.3 g dry wt $\cdot m^{-2}$).

Vegetated intertidal areas — Depending on elevations and size of the beach, these habitats grade into sandflats, mudflats, terrestrial environments, or subtidal areas. Some of the data reviewed below are actually from sediments close to but not within homogeneous vascular plant communities.

Benthic invertebrates living with brackish marsh plants in estuaries are euryhaline species. For example, at the Squamish Estuary, where 76 ha of sedge (*Carex lyngbyei*) are within the intertidal zone (Anonymous 1981), insects (adults and larvae), primarily Chironomidae, are abundant. Two crustaceans, the amphipod *Eogammarus confervicolus* and the isopod *Gnorimosphaeroma oregonensis*, are also dominant. The former species uses a particular microhabitat, namely sedge rhizomes, at Squamish, and high concentrations (up to 14 000 $\cdot m^{-2}$ and 4.6 g dry wt $\cdot m^{-2}$) have been found under the rhizome mat at low tide (Levings 1980b). The mysid *Neomysis mercedis* is found in dense swarms in tidal creeks, for example at the Duck–Barber–Woodward Island marsh complex in the South Arm of the Fraser River (Johnston 1981).

Two species of eelgrass, *Zostera marina* and *Z. americana*, are found in high salinity parts of estuaries and in extensive beds along the west coast of the Strait of Georgia (Harrison 1982). There have been no studies examining the fauna of the beds specifically, but a number of surveys have stations in or close to the vegetation. Eelgrass beds harbor very diverse communities, including representatives of almost all invertebrate taxa in the sea. At high tide, the plants add an additional dimension to the benthic ecosystem, greatly increasing habitat heterogeneity. Ricketts and Calvin (1968) gave details on many of the organisms living in eelgrass beds in United States waters but there are few local data on the species also found in the Strait.

Sibert (1979) examined meiofaunal harpacticoids at the Nanaimo River Estuary obtaining core samples in sandflats with *Z. marina* present in varying density. Over 50 different harpacticoid taxa were identified, including several undescribed taxa, giving a mean abundance of 266 individuals $\cdot 10\ cm^{-2}$ in 400 samples at seven stations. At similar environments at the Cowichan Estuary, mean harpacticoid abundance in cores was about 800 $\cdot 10\ cm^{-2}$ but these data were from only six stations and 18 cores (Sibert et al. 1976). These abundance estimates are within the same order of magnitude as harpacticoid abundance (575 $\cdot 10\ cm^{-2}$ leaf surface, 14 samples) estimated by examining epiphytes scraped from eelgrass leaves on Roberts Bank (C. D. Levings, unpublished data). Core samples in the sediment adjacent to plants obviously can seriously underestimate the local harpacticoid populations.

Larger invertebrates have been studied in eelgrass beds at Boundary Bay and western Roberts Bank by Swinbanks and Murray (1981). Data on density, burrow structures, and/or sediment traces were obtained for the gastropods *Nassarius mendicus* and *Batillaria attramentaria*, the tubiculous polychaetes *Abarenicola pacifica* and *Clymenella torquata*, spionids, the bivalve *Mya arenaria*, and the thalassinidean shrimps *Upogebia pugettensis* and *Callianassa californiensis*. Part of a transect on Roberts Bank sampled at low tide by Levings and Coustalin (1975) passed through eelgrass. Levings (1980c) sampled with a plankton pump within about 1 km of the lower boundary of these eelgrass beds, on ebb and flood tides. The number of species recorded was much higher

than in comparable samples from off Steveston Island in the South Arm of the Fraser. For example, approximately 20 genera of gammaridean amphipods were recorded at Roberts Bank compared with 4 at Steveston Island. At Roberts Bank, megalopa larvae of the Dungeness crab (*Cancer magister*) were observed clinging to drifting eelgrass and were abundant in plankton samples (up to $13 \cdot m^{-3}$). Chang (1975) reported life history observations on the amphipod *Anisogammarus pugettensis* in eelgrass at Roberts Bank and Boundary Bay. This species is one of the most abundant amphipods in these habitats.

Subtidal Habitats Less Than 20 m

The nearshore (<20 m) benthic habitat covers an estimated 1245 km^2 (Table 1) or 18% of the surface area of the Strait. Of this area, 320 km^2 is classified as rocky substrate.

Algal studies prior to 1975 are reviewed by Foreman and Root (1975) and the biology of selected algal species is considered by Carefoot (1977) and Druehl (1981). Two major programs of algal research were initiated in the early 1970's. Austin and Adams (1972) surveyed 42 km between Denman Island and Elma Bay (near the mouth of the Oyster River) as part of a provincial program to evaluate commercially usable red seaweed resources. Their work continued for several years and included the definition of intertidal and upper subtidal algal communities in the northern part of the Strait. One of us (Foreman) initiated a comprehensive benthic ecology program in 1972. Designed to investigate spatial–temporal variations in benthic community structure and function, quantitative and qualitative sampling was accomplished over a 7-yr period (1972–78). Some 600 quantitative samples were obtained in the vicinity of Bath Island to establish seasonal and yearly trends, and a further 400 quantitative samples were collected throughout the Strait as defined by Seymour Narrows and the Canadian–United States boundary. All data (35 000+ species records) were computerized, with more than 300 species of benthic algae and 600 species of benthic fauna quantitatively evaluated. Some results of this study are published (Foreman 1975, 1976a, 1976b, 1977, 1979; Lindstrom and Foreman 1978; Foreman and Root 1975).

Ten algal community types were defined by Foreman (Fig. 4) and used to estimate total algal biomass in the Strait of Georgia and adjacent inlets. Total standing crop ranged from a mean value of 2.94×10^7 kg dry wt, as derived from the quantitative data. Of this, about 85% occurs on rocky substrates. Most of the algal biomass is contributed by less than 20 species of which *Nereocystis luetkeana*, *Agarum fimbratum*, *Laminaria groenlandica*, *L. saccharina*, *Fucus distichus* f. *distichus*, *Constantinea subilifera*, and *Iridaea cordata* f. *cordata* are the major species.

Seaweed decomposition in the vicinity of Bath Island was studied by Smith (1979), who reported a mean peak summer litter accumulation of 5.5 g ash-free dry $wt \cdot m^{-2}$ and concluded that most litter undergoes decomposition near its place of deposition. Using a deterministic simulation model to predict rate of detritus formation and soluble matter release from decomposing seaweed litter, Smith determined 56% of decomposing litter formed detritus and 44% was released as soluble matter.

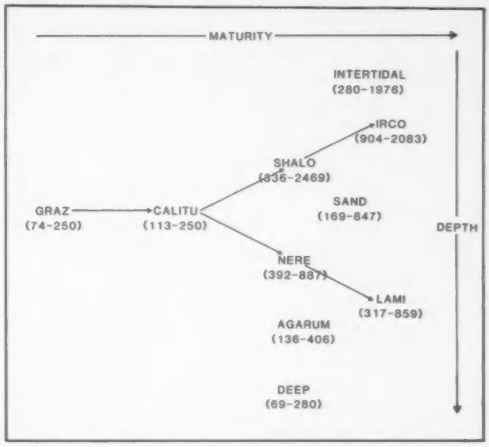

FIG. 4. Ten algal community types, as defined by Foreman, which occur in the Strait of Georgia and adjacent inlets with mean and maximum dry weights (in grams per square metre) shown in parentheses. Successional sequence shown with arrows. GRAZ represents an urchin grazed bottom with few algal species; CALLTU is similar to GRAZ except for the dominance of *Calliarthron*; SHALO is a foliose red algal community ultimately, at shallower depths, dominated by *Iridaea* and *Constantinea* (IRCO); NERE is a *Nereocystis*-dominated community with red algal dominated understory, and this type is gradually replaced by the perennial *Laminaria* (LAMI) with a reduced red algal understory; AGARUM is dominated by *Agarum*; DEEP consists of a collection of red algal species, mainly filamentous, dominated by *Weeksia* and *Stenogramme*; the SAND community type is determined by the substrate that, in this instance, often includes rocks and is dominated by *Zostera* and *Gracilaria*.

D. Garbary (Department of Botany, University of British Columbia, Vancouver, B.C., personal communication) has completed an extensive study of algal distribution, seasonality, and phenology in Burrard Inlet and adjacent waters. This study increases the number of algal species known to occur in the Strait of Georgia to between 325 and 350.

Nearshore benthic faunal studies are limited. Ellis (1967a, 1967b, 1968a, 1968b, 1968c) conducted several grab surveys in the southern end of the Strait and a few shallow locations were sampled.

The most comprehensive faunal collection from shallow rocky substrates is that from Foreman's 7-yr program covering the entire Strait and adjacent inlets. These data are largely unpublished. A preliminary analysis of 2 yr of data from Bath and Sear islands is under preparation by Keen and Foreman. In 1972, 392 taxa were found in 124 quantitative quadrats; in 1973, 286 taxa were enumerated from 64 quadrats. Five preliminary faunal assemblages were described by multivariate analysis (Table 2) in terms of depth and substrate type from a total of 188 quadrats. The faunal assemblages are compared with the six algal communities defined by Lindstrom and Foreman (1978) in Table 3, with many invertebrates within these groups showing strong association with algal communities.

TABLE 2. Preliminary faunal groups identified by multivariate analysis of 188 quantitative quadrats collected in the vicinity of Bath and Sear islands (R. E. Foreman, unpublished data).

Group	Depth (m)	Substrate	Dominant invertebrates
I	0–5.5	Continuous rock	*Balanus glandula*,[a] *Mytilus edulis*,[b] associated gastropods and polychaetes
II	6.0–9.0	Continuous rock	*Vermiliopsis*,[c] *Hermissenda crassicornis* *Adalaria* spp.,[d] *Harmothoe multisetosa*[e]
III	4.5–8.0	Rock	*Lacuna marmorata*, *Lacuna carinata*,[f] *Margarites costalis*,[f] *Bittium escherichtii*,[f] *Platynereis bicaniculata*,[e] *Hippodiplosia insculpta*,[g] *Peisidice aspera*,[e] *Eteone tuberculata*,[e] *Lumbrinereis pellida*,[e] *Balanophyllia elegans*,[h] *Nassarius mendicus*,[f] *Capitella capitata*,[e] *Prionospio malmgreni*,[e] *Ammotrypane aulogaster*,[e] *Caprella laeviuscula*,[i] *Parvilucina tenuisculpta*[h]
IV	9–13	Continuous rock	*Peisidice aspera*,[e] *Eteone tuberculata*[e] *Lumbinereis pellida*,[e] *Balanophyllia elegans*,[h] *Nassarius mendicus*[f]
V	4.5–11	Mixed substrates (sand–mud–rock)	*Capitella capitata*,[e] *Prionospio malmgreni*,[e] *Ammotrypane aulogaster*,[e] *Caprella laeviuscula*,[i] *Parvilucina tenuisculpta*[f]

[a]Crustacea–Cirripedia.
[b]Mollusca–Bivalvia.
[c]Polychaeta–Sedentaria.
[d]Mollusca–Opistobranch.
[e]Polychaeta–Errantia.
[f]Mollusca–Gastropoda.
[g]Bryozoan.
[h]Coelenterata.
[i]Crustacea–Amphipoda.

The green sea urchin, *Stronglyocentrotus droebachiensis*, can be one of the most influential animals in the shallow subtidal rocky communities in the Strait. In 1973, in 21 populations examined by Foreman and Lindstrom (1973), mean abundance was $322 \cdot m^{-2}$ (SD = 228) and mean biomass was 5770 g wet $wt \cdot m^{-2}$ (SD = 6065). This level of abundance is highly episodic. Foreman (1977) suggested that the increase in *S. droebachiensis* populations in the Strait probably resulted from a favorable plankton bloom in the spring of 1969, following the suggestion of Himmelman (1979) (see p. 1134), as to factors initiating spawning, coupled with an unusually long period of cool water temperatures. Sea urchin larval development is best at low water temperatures (Stephens 1972).

Sea urchin outbreaks are responsible for localized perturbations of the benthic algal community. Foreman (1977) quantitatively compared the impact of such an outbreak with a nongrazed control. The primary effects were a selective elimination of 60% of the algae, 65% reduction in mean dry weight per square metre, and a 60 % reduction in Shannon–Weiner species diversity. In postgrazing years, transient algal species were significantly higher in the grazed site and biomass was the only variable to recover to pregrazing levels within 3 yr. The abundance of *Nereocystis luetkeana*, an annual kelp species in the Strait, appears to be influenced by such perturbating events initiating cyclical changes in biomass. Similar effects are noted in the benthic fauna, with a dramatic reduction in species richness, as shown in Table 4. The elimination of algal cover exposes extensive areas of substrate and large subtidal settlements of mussels and barnacles were noted. Therefore, one of the most dramatic effects of urchin grazing may be the sudden increase in available primary space, which is the limiting resource for many sessile organisms.

Cabot (1979) quantitatively characterized a subtidal gastropod assemblage in the vicinity of Bath Island. Ninety-five percent of all individuals collected were found to belong to five species, and most species attained their maximum development after recruitment in the spring or early summer. Diversity, species richness, total abundance of gastropods, and densities of several species were correlated to the abundance of benthic diatoms.

Scuba techniques were also used by Lim (1980) in work to survey macrofauna and habitats at 42 sites around the perim-

TABLE 3. Coincidence matrix (Stephenson et al. 1970) showing the percentage of species from each of the five animal groups that were associated with each of the six algal groups defined by Lindstrom and Foreman (1978) (R. E. Foreman, unpublished data).

	Algal group					
Animal group	Sand	Foliose red	Kelp	Inter-tidal	Deep	Turf
I	2	30	4	58	4	3
II	1	22	48	2	27	—
III	5	42	22	6	20	6
IV	10	15	14	2	54	4
V	19	29	22	3	24	3

eter of Saltspring Island. She decided that four habitats could be distinguished on the basis of slope, sediment type, and vegetation: (1) gently sloping (5°) sand–shell silt, (2) eelgrass beds, (3) steep (50°) rock faces with sand–shell at their base, and (4) broken rock and sand–shell. There were obvious differences in the dominant organisms at the various sites, although only presence-or-absence data were given.

Beak-Hinton Consultants Ltd. (1977) sampled soft bottom benthos on four transects on southern Roberts Bank at 5-m intervals from 0 to 50 m. An interpretation of these data showed that the numerical abundance of polychaetes in the samples reached a maximum at 5 m, coinciding with a peak in fine material in the sediments (C. D. Levings, unpublished data).

SUBTIDAL HABITATS GREATER THAN 20 M

Basins — Ellis (1968c) described the macrofauna from a station off Nanaimo (POG 1, 402 m) characterized by fine material (>90% silt), which is typical of sediment in the deep basins. In terms of both density and biomass, as measured by grab samples, echinoderms, molluscs, and polychaetes dominated the samples. The holothurians *Molpadia intermedia* and *Chiridota* sp. and the heart urchin *Brisaster latifrons* were among the dominant organisms. Prominent molluscs were the gastropod *Acteocina* sp., the bivalve *Yoldia thraciaeformis*, and the scaphopod *Dentalium* sp. The abundant polychaetes were *Laonice cirrata*, *Lumbrinereis* sp., and *Nephtys* sp. A somewhat similar suite of species was observed in trawls and grabs off Point Grey (250 m) in the southern Strait by Hoos (1977) and Packman (1980). Trawl surveys showed that *Chiridota* sp. was particularly abundant. Camera data from contiguous habitats in outer Howe Sound showed that abundance of this species ranged up to $55 \cdot m^{-2}$ (McDaniel et al. 1976).

Bernard (1978) has provided a summary of benthic community types in the Strait as judged from the macrofauna at approximately 300 stations sampled with dredges. According to this author, six communities could be described by their dominant species as follows: (1) *Osteocella* (Coelenterata)/Sipuncula, (2) *Paracaudina* (holothurian)/*Compsomyax* (bivalve), (3) *Brisaster* (heart urchin)/*Lucina* (bivalve)/*Aphrocallistes* (Porifera), (4) *Acila*/*Nemocardium* (bivalves), (5) *Glycymeris*/*Chlamys* (bivalves), (6) *Glycera* (Polychaete)/*Macoma* (bivalve). The distribution of the communities is shown in Fig. 5. As noted by Bernard (1978) more varied communities are present in areas of mixed sediment and rock outcrops, such as Halibut Bank, where his *Glycymeris*/*Chlamys* community was found. Levings and McDaniel (1974) found that certain epilithic organisms such as the anemone *Metridum senile* were growing on a telephone cable in the middle of the southern Strait where fine sediments are the common substrate. Ellis (1969) sampled with grabs at two stations in outer Burrard Inlet (43, 70 m) where sand and mud characterized sediments. Polychaetes (e.g. *Hemipodus borealis*, *Lumbrinereis* sp., *Nephtys* sp., *Laonice cirrata*, *Maldane glebifex*, *Phyllochaetopterus* sp., *Pista cristata*, *Sternaspis fossor*, and *Terebellides stroemi*), crustaceans (unidentified amphipods), bivalves (*Macoma elimata*, *Psephidia* sp., and unidentified pelecypods), and echinoderms, (*Ophiura sarsi* and *Molpadia intermedia*) were reported as "ecologically significant" species in the communities in these habitats. Biomass of the assemblage was about 14 g dry $wt \cdot m^{-2}$.

TABLE 4. Reduction in number of taxa of various faunal groups pre- and postgrazing by sea urchins (*S. droebachiensis*) at Bath and Sear islands (from Keen and R. E. Foreman, unpublished data).

Taxa	1972 (pregrazing)	1973 (postgrazing)
Isopoda	1	0
Gastropoda	13	0
Amphipoda	4	0
Bryozoans	2	0
Decapod crabs	6	1
Caprellid amphipods	2	0
Limpets	4	1
Polychaetes	4	2
Chitons	4	0
Bivalve molluscs	2	1
Decapod shrimp	1	0
Starfish	0	1

Channels — Dunnill and Ellis (1969) found a very high density and diversity of *Macoma* spp. off Moresby Island, near the east end of Satellite Channel. The mean biomass of all macomas taken with a Van Veen grab was 114 g dry $wt \cdot m^{-2}$. The mean number of different species of *Macoma* occurring in samples off Moresby Island on silty sands was

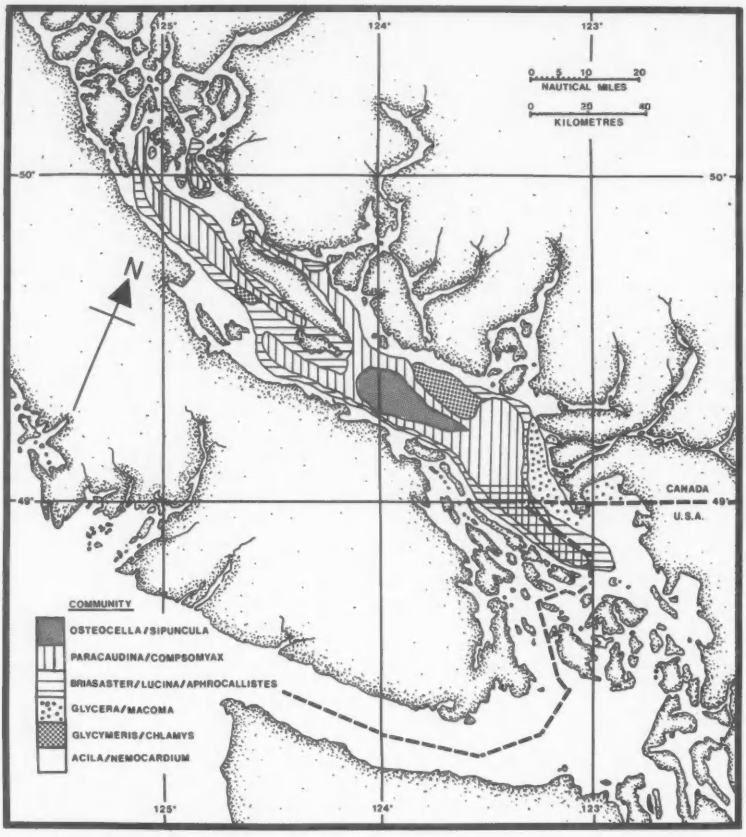

FIG. 5. Communities of macrobenthos in the major basins of the Strait of Georgia, based on interpretations of dredge samples. The apparent predominance of the *Acila/Nemocardium* community is associated with reduced density of sample points near to shore (from Bernard 1978).

5.3 compared with only 1.7 on "shell-gravel." Similar differences in molluscan fauna between sediment type in the area were recognized by Popham and Ellis (1971) using cluster analysis techniques. Ellis (1969) sampled in Satellite Channel (77 m) at a station where sediment type was approximately 60% sand and 40% silt and clay. The following taxa were reported as "ecologically significant" species on three or more trips: the polychaetes *Lumbrinereis bifurcata*, *Nephtys* sp., *Maldane glebifex*, *Pista cristata*, *Prionospio* sp., and *Sternaspis fossor* and the bivalves and the echinoderms *Ophiura sarsi*, *Brisaster latifrons*, *Molpadia intermedia*, and *Pentamera lissoplica*. Benthic biomass was approximately 60 g dry $wt \cdot m^{-2}$ (Ellis 1971).

The axis of Stuart Channel, between the north end of Saltspring and Vancouver islands, is characterized by finer sediments (96% silt−clay) at depths of about 200 m (Ellis 1968a). Dominant organisms include the heart urchin *Brisaster latifrons*, the echiuroid *Bonellia* sp., the bivalve *Yoldia thraciaeformis*, and the polychaetes *Nephtys* sp. and *Terebellides stroemi*. Mean biomass (three samples) was 17 g dry $wt \cdot m^{-2}$.

Fjords — The fjords of British Columbia provide an unusual opportunity to study a habitat that is rarely accessible: that of the deepwater benthos of hard substrata. The manned submersible *Pisces IV* has been used extensively to study the vertical cliffs of the fjords. Large numbers of photographs supply the necessary samples for analysis of community composition. Animals down to 1 cm in diameter can be readily recognized and collections complement the identifications. Observations presented here result from *Pisces IV* dives made in 1981−82 in Jervis Inlet (13 dives), Howe Sound (4 dives), and Saanich Inlet (37 dives) (V. J. Tunnicliffe, unpublished data).

The composition of the epilithic benthos in each of these inlets is presented in Table 5. Because of the large discrep-

TABLE 5. Hard substratum communities of lower British Columbia fjords (V. J. Tunnicliffe, unpublished data).

Fjord	Features	Faunal dominance	Cover	Diversity	Community type
Saanich Inlet	230 m, frequently O_2 depleted	Serpulid, ascidean, sponge	85% (max.)	High	Mainly filter feeders, few predators
Jervis Inlet	680 m, clear, stable water	Serpulid, sponge, brachiopod−coral	30% (min.)	Low	Nonselective suspension feeders, many predators
Howe Sound	286 m, inner basin O_2 depleted	Inner: coral and ascidean; outer: coral and brachiopod	40% (est.)	Moderate	Many selective suspension feeders and detritivores

ancies between the numbers of observations made in each inlet the chances of encountering rarer species vary and systematic comparisons are difficult. However, some gross differences were evident and represent trends in local community structure.

Most dives in Jervis were made in the lower inlet where unbroken cliffs extended to 600 m. The granodiorite surfaces accumulate little silt and provide clear substrata for settling larvae. The deepwater fauna is dominated by scleractinian cup corals (*Caryophyllia alaskensis*) and brachiopods (*Laqueus californicus*). In midwater depths soft corals and glass sponges become very common creating a striking three-dimensionality to the cliff community. Above 200 m, serpulid polychaetes and encrusting sponges are dominant. In all these fjords, the photic zone supports an algal dominated community down to about 50 m in depth. Jervis is particularly notable for the abundance of coelenterates (hard and soft corals as well as anemones and hydroids) and glass sponges. The Hexactinellida are usually restricted to deep or polar waters; their abundance and accessibility in British Columbian fjords is puzzling but has lead to enlightening studies of these poorly known animals (Reiswig 1980; Lawn et al. 1981).

Among the mobile benthos, asteroids of numerous species are commonly sighted. They appear to be particularly partial to sponge meals, glass or otherwise. The detritivorous galatheid crabs, *Munida quadrispina*, are abundant, particularly in the debris of the glass sponges. In places, the sponge growth is so prolific that ledges are piled high with skeletons that are essentially woven silica. The fauna of these "reefs" is intriguing, particularly in such forms as *Thelepus cincinnatus*, a terebellid polychaete that builds its tube with sponge spicules.

The faunal composition of the outer basin of Howe Sound is highly reminiscent of the shallow part of Jervis Inlet. Brachiopods and serpulids are common but large numbers of glass sponges (especially *Aphrocallistes vastus*), the gorgonian *Paragorgia arborea*, and the anemone *Metridium senile* distinguish this area from the inner Sound. Clonal growths of a stoloniferan coral cover large areas of the walls between 160 and 180 m.

The epilithic community of the inner basin is undoubtedly influenced by detrital input from the Squamish River (Syvitski 1980) and frequent low dissolved oxygen levels. Some reflection of the fatalities among the soft sediment benthos (Levings 1980a) can be expected in the epilithic benthos. The fauna is strongly dominated by cup corals and ascideans; none of the soft corals and few of the sponges outside the sill grow here. There are few echinoderms although the galatheid *Munida* is common both on the bottom and on the cliff.

The fauna and dynamics of Saanich Inlet appear to be more complex due, perhaps, to the fluctuating oxygen levels. Tunnicliffe (1981) recorded a higher diversity in the epibenthos of the dysaerobic zone (<2 mL $O_2 \cdot L^{-1}$) than at the base of the photic zone. The cliffs are devoid of fauna from the bottom to about 130 m (Tunnicliffe 1981). There is a suggestion, however, that these waters were once well oxygenated; the basal attachments of the glass sponge *Aphrocallistes vastus* can still be seen on the lower cliffs although live specimens are presently restricted to less than 70 m (where year-round dissolved oxygen is usually greater than 2.0 mL $\cdot L^{-1}$) in Saanich. The first animals to appear at 125 m are small Hadromerid sponges and an anemone of the family Actinernidae. These animals and a number of ascideans and brachiopods experienced prolonged exposure to anoxic water during 1980. Community domination changed from sponges to ascideans at 75 m. A different assemblage of encrusting sponges as well as serpulids is present in shallower water but the glass sponges, mainly *Rhabdocalyptus dawsoni*, are never common. Mobile predators such as rock fish and echinoderms are virtually absent below 75 m. The galatheid crab, *Munida*, is abundant and the deep population seems well adapted to low oxygen levels.

The glass sponge−soft coral growths in Jervis and outer Howe Sound were similar. There, predatory molluscs, echinoderms, and fish were present. In contrast, the community of the dysaerobic zone in Saanich is dominated by ascideans and demosponges and there are few predators present. Periodic oxygen stress is experienced in both Saanich and the inner basin of Howe Sound; interestingly, solitary ascideans are very abundant in the dysaerobic zones of both inlets. The community characteristics of these three fjords are presented in Table 5. Diversity values calculated for these communities

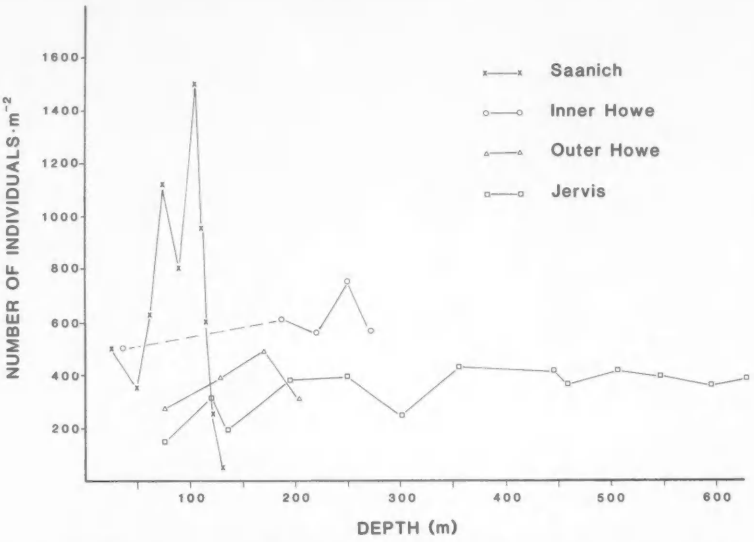

FIG. 6. Changes in abundance of epilithic fauna with depth in Saanich Inlet, Howe Sound, and Jervis Inlet (V. J. Tunnicliffe, unpublished data).

indicate that Saanich is somewhat higher but the values fall within similar ranges. Contribution to diversity in Saanich is due mainly to species richness: in the biotic zone from 3 to 120 m, 58 species were encountered compared with the zone between 30 and 620 m in Jervis in which only 8 more species were recognized. A large contribution to the diversity of the Jervis community is from species evenness.

The abundances of the epilithic faunas of the fjords are illustrated in Fig. 6. Saanich shows remarkably dense populations above the anoxic zone. Cover estimates (amount of space occupied estimated from point counts of standardized photographs of cliff walls) were as high as 80% in this zone, suggesting intense competition for space. In Jervis and outer Howe Sound, however, rock cover by all animals was consistently below 50%. Within Howe Sound itself, organism density in the inner basin was significantly higher than that in the outer basin (t-test, $P = 0.05$). Prolific animal growth in Saanich and inner Howe was surprising in view of literature reports of depauperate communities in areas of depleted oxygen (i.e. Kitching et al. 1976; Rosenberg 1980). The water just above the anaerobic zone is, however, one of intense bacterial (Emerson et al. 1979) and zooplankton (Devol 1981; Mackie and Mills 1982) production; particulate-feeding benthos are most abundant in this zone. Inner Howe Sound receives a large amount of detritus from glacial runoff (Syvitski 1980), which may provide a necessary carbon source. Excessive suspended particulate loads can, however, be a deterrant to the development of fjord benthos (Farrow et al. 1983).

System Interactions

PHYSICAL INFLUENCE

Numerous variables may affect the arrangement and functioning of benthic assemblages, such as temperature, salinity, light, dissolved gases, nutrients, depth, currents, wave action, and sediments. Bousfield (1957) and Lewis and Quayle (1972) recognized the last two as features that distinguished the biota of the outer coasts of British Columbia from that of the Strait in which organisms are adapted to sheltered, brackish, and turbid environments. In the Fraser River Estuary Chapman and Brinkhurst (1981) documented seasonal changes in benthos in the channel of the North Arm, with special reference to oligochaetes and interstitial salinity. Levings (1980c) showed how marine zooplankton communities in the salt wedge merge with estuarine epibenthos in the deeper channels (up to 10 m) of the South Arm.

Whether or not abundance or presence of a benthic organism can be predicted from sediment parameters is a complex issue that has been reviewed thoroughly elsewhere (e.g. Gray 1974). Sediment characteristics such as size, sorting, organic content, and microbial populations frequently influence both adult and larval settling behavior. In our study area there have been only a few studies on this topic. Dunnill and Ellis (1969) investigated the distribution of seven species of the bivalve genus *Macoma* in Satellite Channel. Despite the wide variation in sediment type found in the study area few clear-cut differences were found in the distribution of the species. Comparatively larger individuals of *M. brota*, *M. calcarea*, *M. elimata*, and *M. lipara* were found in sediments with silt–clay content between 15 and 50%, indicating these species were adapted to finer sediments. *Macoma incongrua* was the only species regularly found on "shell-gravels" at stations exposed to strong currents. However, the largest individuals of the species were found at stations where currents were weaker. *Macoma carlottensis* was found on the widest variety of sediment types (9–95% silt and clay), sug-

gesting this species is relatively insensitive to sediment conditions. Reid and Reid (1969) concluded that three feeding types were present among these seven species, namely deposit feeders, suspension feeders, and a feeding mode where surface films of bacteria on sand grains were used.

McGreer (1979) studied a population of *M. balthica* on a part of Sturgeon Bank affected by sewage pollution. One of the limiting factors for the bivalve was thought to be the extremely high concentrations of organic material (sludge) and heavy metals in the sediments. *Macoma balthica* and the amphipod *Corophium salmonis* exhibited some degree of discrimination for sediment type when tested in the laboratory (Chang and Levings 1976). However, these were adult organisms and it is generally acknowledged that larval survival is more relevant for interpreting field distributions, especially for almost sedentary organisms such as bivalves. Harrison (1981) found that harpacticoid assemblages in sand on northern Sturgeon Bank changed when mud concentrations increased due to freshet effects. Competition and feeding strategies were suggested as possible mechanisms leading to the changes.

The sills of the lower British Columbian fjords support an unusual array of epibenthic communities that develop in response to local sediment and hydraulic conditions. The shallow sill of Knight Inlet experiences tidal currents in excess of 1 $m \cdot s^{-1}$ (Pickard and Rodgers 1959) and the surficial sediments are cobble to boulder sized. Forests of the gorgonian coral *Primnoa willeyi* have formed on the sill crest and frequently grow large enough to initiate movement of the boulders themselves (Tunnicliffe and Syvitski 1983). These large polyped suspension feeders take advantage of the dense populations of planktonic crustaceans in the water layer just above the sill. The inner sill of Howe Sound rarely sees currents in excess of 20 $cm \cdot s^{-1}$ (Bell 1975) but dense coral growths, this time the sea whips *Osteocella septentrionalis* and *Virgularia tuberculata*, have established in the silts of the sill crest. Numerous glass sponges (*Aphrocallistes vastus*) form ramparts in the sediment atop the sill. The sill of Saanich Inlet experiences variable currents to 65 $m \cdot s^{-1}$ (Herlinveaux 1968). In the areas of lower currents ophiuroids, sea pens (*Ptilosarcus gurneyi*) and octopus are abundant; the current-swept rocks are populated primarily by *Metridium senile* and scallops.

Pelagic to Benthic Coupling

As pointed out by Hargrave (1973) and others, the mechanisms whereby organic material produced in the photic zone reaches the bottom are an important influence on production and composition of benthic communities. For example, Hargrave and Peer (cited in Parsons et al. 1977) showed a linear relationship between macrobenthic biomass and chlorophyll *a* in overlying waters. Important influences on benthic assemblages include sedimentation rates, provenance, and composition but there are few data from our study area and none apparently from the main body of the Strait.

Iseki et al. (1980) found that sedimentation rate per trap in Saanich Inlet was about 3.3 mg $C \cdot d^{-1}$ (125 cm^2 area; mean of eight samples, March and April 1978). Syvitski's (1980) data from the Squamish Estuary, head of Howe Sound, were from time periods well past the annual phytoplankton bloom. At this turbid estuary, sedimentation of inorganic material was very high, with an average value of 407 $mg \cdot 125\ cm^{-2} \cdot d^{-1}$ at 5 m (nine samples) during April–October 1977. The overall rate of sedimentation at such estuaries is in direct response to river discharge. Syvitski and Murray (1981) described "biogenic agglomerates," which result from the interaction of sediment, bacteria, and phytodetritus. These agglomerates are no doubt formed off the mouth of the Fraser River, where turbidity levels are also high (Milliman 1980). Together with zooplankton pelletization, also investigated by Syvitski and Murray (1981) in Howe Sound, agglomeration is probably an important mechanism in transporting food to the level bottom communities in the main body of the Strait (Fig. 7).

Mass sediment movement can also have a considerable effect on infaunal benthos. At the Fraser, Squamish, and Homathko estuaries sandflows have been documented, and these phenomena are related to river freshets (see Milliman 1980 and Syvitski and Murray 1981 for information on the respective locations). In the Squamish Estuary Pomeroy (1977) estimated that the sedimentation rate was approximately 2.0 $cm \cdot yr^{-1}$. As shown by a number of authors (Stephens et al. 1967; Seki et al. 1968; Naiman and Sibert 1978) movement of material into the Strait via rivers is dependent on runoff cycles. River discharge can also bring invertebrates into estuaries, as shown for the Squamish River (Levings 1973) and Berkeley Creek at Departure Bay (Williams 1979). For glacier- and/or snowmelt-fed rivers on the east side of the Strait (e.g. Squamish, Homathko) the input of material can occur both in spring and autumn, the latter runoff generated from heavy rains. For other rivers, river freshets are generated by rain and tend to occur only in fall and winter. The biological implications of these differences in runoff have yet to be explored.

The shoreline length in the Strait is considerable (see Table 1) because of island and fjord configurations, and therefore, primary production of the nearshore area must also be considered as major inputs, especially to the shallow water and littoral benthos. This was recognized by Stephens et al. (1967) who showed two seasonal peaks in sedimentation in Departure Bay. The first peak occurred about 2 mo after the spring phytoplankton bloom and consisted largely of phytogeneous material. Sedimentation rate was about 1.3 mg $C \cdot 125\ cm^{-2} \cdot d^{-1}$. The second maximum, with about the same sedimentation rate, was from terrigeneous and nearshore areas and occurred from October to December. Using a marine bacterium as an assay organism, differences in amounts of nutrients and carbohydrates available were observed with sediments from the two time periods (Seki et al. 1968). Subsequently, the following sources of organic material for nearshore benthos have been identified by various authors: decaying kelp (Albright et al. 1980; Smith 1979), leaf litter and riverine input (Seki et al. 1969; Naiman and Sibert 1978), sedge (Pomeroy 1977), eelgrass (Naiman and Sibert 1978), and microbenthic algae (Pomeroy and Levings 1980).

In addition to providing a direct supply of energy for growth of benthos, there is some evidence that phytoplankton sedimentation can stimulate spawning in certain

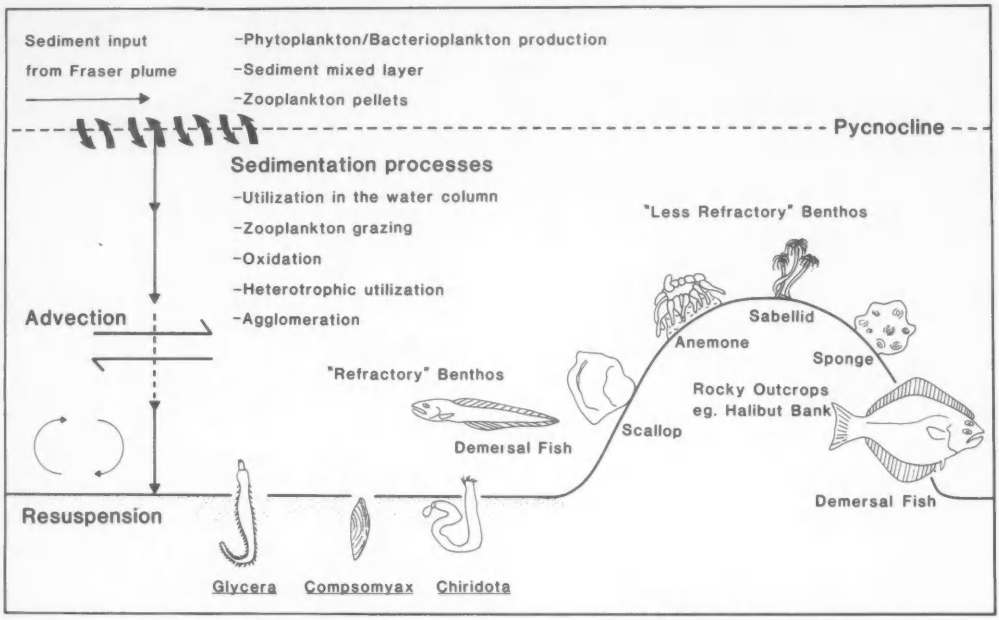

FIG. 7. Physical processes involved in benthic–pelagic coupling and fauna in the major basins of the Strait of Georgia.

invertebrates. This was shown by Himmelman (1979) for two chitons (*Tonicella insignis* and *T. lineata*) and the green urchin *S. droebachiensis* at First Narrows and Eagle Harbour (near West Vancouver) and Porteau (Howe Sound).

The fauna of fjords can be greatly influenced by high suspended particulate loads from glacial meltwater. Farrow et al. (1983) described the shift in feeding mechanisms shown by members of the cliff benthos in Knight Inlet. Moving down inlet away from the major sediment input, suspended particulate load decreases logarithmically and the feeding type changed from nonselective suspension feeders to filter feeders that are able to take advantage of a larger organic fraction without clogging.

Transport of food to benthic communities is of course heavily influenced by tidal currents, which is also reflected in changes in feeding types of benthic species. Such changes might be expected, for example, in the rocky subtidal communities in the various passes between the Gulf Islands and at the northern end of the Strait (Seymour, Yuculta Narrows). More filter feeders such as the giant barnacle (*Balanus nubilus*) might be expected in areas of strong currents (McDaniel 1973).

BENTHIC TO PELAGIC COUPLING AND FISH FOOD WEBS

There are numerous ways in which the benthic community contributes to the support of pelagic organisms. Meroplankton is a research topic that has received little attention; it represents a community that links pelagic and benthic habitats. Counts of the zoea larvae of decapods and the cyprid stage of barnacles are frequently reported in data listings for both planktonic (e.g. Fulton et al. 1969b) and epibenthic (e.g. Levings 1980c) surveys, but there has been no synthesis of the available data. Oyster larvae surveys are conducted annually to predict spatfall (see Ketchen et al. 1983) but the contribution of molluscan and other noncrustacean larvae is generally not considered in pelagic productivity studies. Planktonic larvae are subject to the same physical forces as phytoplankton and/or zooplankton, and oceanographic factors influencing larvae in turn can be related to distribution of adults. For example, Yamada (1977) concluded that southward flowing currents were partially responsible for the absence of the gastropod *Littorina planaxis* in the Strait of Georgia. Specimens transplanted from California to Vancouver Harbour and to San Juan Island survived; temperature and salinity cannot be invoked as limiting factors.

On foreshores and estuaries, particulate and dissolved organic carbon originating from vascular plants, benthic algae, phytoplankton, and heterotrophic production by bacteria is involved in the food webs of invertebrates (Fig. 8). Fish use of the invertebrates at high tide, other than that by juvenile salmonids, is almost completely undocumented. Studies on Roberts Bank (Greer et al. 1980) have shown that postlarval and juvenile lemon sole (*Parophyrs vetulus*) and starry flounder (*Platichthys stellatus*) are major users of eelgrass beds and adjacent sandflats. A similar situation is expected at Baynes Sound, where a significant lemon sole fishery existed some years ago (Ketchen et al. 1983). Some data on noncommercial bottom feeders, specifically the blackbelly eelpout (*Lycodopsis pacifica*) and the cockscomb

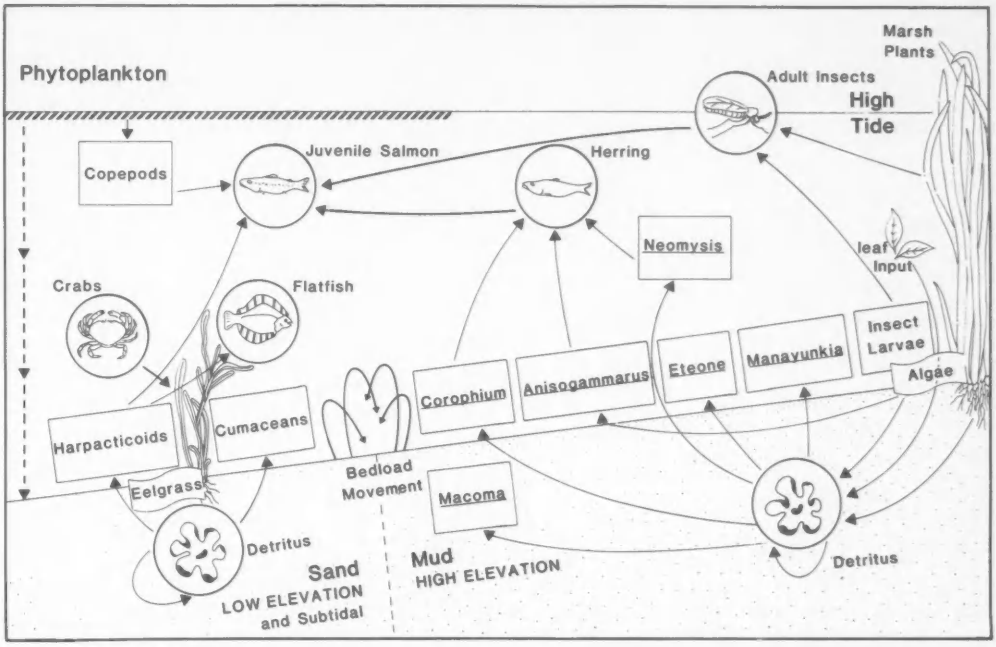

FIG. 8. Food webs and important processes relating trophic levels at an idealized estuary or foreshore habitat, Strait of Georgia.

prickleback (*Anoplarchus purpurescens*), are available. The eelpout was found to be a soft bottom benthic feeder, using amphipods, polychaetes, and small bivalves in outer Burrard Inlet (Levings 1968). The cockscomb prickleback, an intertidal species, used algae (e.g. *Ulva lactuca*) as food as well as crustaceans (Peppar 1965).

Since 1972 there have been a number of studies, of varying intensities, investigating the diet of juvenile salmonids in intertidal areas of the Strait. This work has shown linkages from salmon to benthic communities through a variety of fauna, primarily crustaceans and insects. The diet of juvenile salmon on or within 1 km of beach environments has been examined at the following locations in the Strait: Fraser Estuary (Goodman 1975; Dunford 1975; Levy et al. 1979; Levy and Northcote 1981; Levings 1981), Burrard Inlet (Goodman 1975), Squamish Estuary (Goodman and Vroom 1972; Levy and Levings 1978), Campbell River Estuary (Goodman and Vroom 1974), Southern Baynes Sound (Fraser et al. 1979; Mason 1974), Oyster River Estuary (Goodman 1974), Nanaimo Estuary (Healey 1979, 1980, 1982; Sibert and Kask 1978), Departure Bay (Godin 1981), and Cowichan (Anonymous 1980).

Sibert and Kask (1978) compared chinook diets from the foreshore portions of the Nanaimo, Campbell, Cowichan, and Fraser estuaries. A significant positive correlation was found in diets between Nanaimo and Cowichan, a weak positive relationship between Campbell and Nanaimo, and weak negative correlations in the other comparisons (Table 6). Intertidal habitats characterized by marked freshwater effects, either because of relatively high river discharges (e.g. Squamish and Fraser estuaries) or local physiography (e.g. Campbell Estuary) support euryhaline floras and faunas. Flora such as sedges predominate with accompanying insect communities and crustaceans such as the mysid *Neomysis mercedis* and the amphipod *Eogammarus confervicolus*. Insects and the latter epibenthic crustaceans feature highly in juvenile salmon diets at these locales. Where river discharges are smaller and freshwater is dispersed (e.g. Nanaimo and Cowichan estuaries), eelgrass, a more stenohaline plant, characterizes intertidal vegetation. Diets of salmon are typically more diverse at these locations, using harpacticoids associated with eelgrass, nauplii of barnacles, decapod larvae, and zooplankton advected onto tidal shores (e.g. the cladoceran *Podon* spp., the calanoid copepod *Eurytemora*, etc.).

These habitat subdivisions, and corresponding prey availability, frequently occur within an estuary because of transverse patterns of salinity and deflection of river water by natural and manmade features. Southern Roberts Bank on the Fraser Estuary is characterized by relatively stenohaline vegetation such as *Zostera marina* and *Salicornia virginica*, whereas Sturgeon Bank, closer to the main discharge of the South Arm, supports such brackish marsh species as *Carex lyngbyei* and *Scirpus* spp. together with extensive sandflats (Yamanaka 1975; Swinbanks 1979). The ranked numerical abundance of invertebrates in chinook (*Oncorhynchus tshawytscha*) fry diet (May 1980; $N = 15$) reflect these

TABLE 6. Correlations between diets of chinook salmon (*O. tshawytscha*) at the Cowichan, Campbell, Fraser, and Nanaimo estuaries (from Sibert and Kask 1978).

	Nanaimo	Cowichan	Campbell	Fraser
Cowichan	+0.762	—		
Campbell	+0.133	−0.058	—	
Fraser	−0.054	−0.009	−0.220	—

differences: Sturgeon Bank: adult dipterans, *Eurytemora* spp., unidentified calanoid copepods, *Metridia* sp., and the cumaceans *Lamprops quadriplicata* and *Cumella vulgaris*; Roberts Bank: the harpacticoid copepods *Tisbe* sp., *Harpacticus* spp., benthic gammarids, *L. quadriplicata* (C. D. Levings, unpublished data).

Fish feeding studies at nonembayed estuaries and other types of nearshore habitats such as rocky shores, sandy beaches, and kelp beds have received little attention in the Strait. These alternatives to embayed estuarine habitat need more research effort before generalizations or even adequate descriptions are possible. In late spring and summer of 1969 and 1970, juvenile pink (*Oncorhynchus gorbuscha*) and chum fry (*O. keta*) at southern Baynes Sound mainly used pelagic copepods, but pink used harpacticoid copepods almost exclusively between April and June 1970 (Fraser et al. 1979). Pink fry on rocky beaches at Departure and Hammond bays near Nanaimo used barnacle nauplii and harpacticoid copepods extensively (Godin 1981). The few chinook smolts caught near the mouth of the Oyster River, a good example of a nonembayed estuary, were using terrestrial invertebrates (Goodman 1974) in contrast with the chum, pink, and coho that were feeding on pelagic copepods. Some of these food web relationships are shown diagrammatically in Fig. 8, which portrays an idealized estuary or foreshore with several of the above habitats present.

The deeper benthic habitats in enclosed seas such as the Strait and in fjords are characterized by organisms with relatively high standing crops, which apparently have very slow turnover rates and are relatively unproductive compared with shallower species. The former, termed refractory species by Matthews and Heimdal (1980), do not support major populations of bottom fish. This appears to be the case in the Strait, judging from recent commercial fishing patterns. Pearson (1980) recently reviewed the data relating to the inverse relationship between depth and benthic biomass in fjords.

Conclusions

Although the major assemblages of benthos of the Strait of Georgia have been described, there is little information on the dynamics of benthic communities, secondary production of zoobenthos, benthic−pelagic couplings, or the quantitative relationships between oceanographic variables and benthic production. The available local data on secondary production are given in Table 7. Rocky intertidal filter feeders (barnacle, oysters) are more productive than detritivores such as estuarine harpacticoids, mudflat bivalves, and deepwater polychaetes. The use of these various organisms by predators such as fish has been explored only in a few locations (such as the Nanaimo Estuary). There have been no other integrated studies in which several trophic levels have been examined simultaneously.

The processes relating fish and benthic communities to overlying and adjacent production systems for the deep basin (Fig. 7) and soft sediment foreshores (Fig. 8) illustrate interactions that we feel are of major importance and worthy of expanded research efforts.

Depth is a major parameter affecting food supply to the benthos of the basins. For example, Halibut Bank (Fig. 1), which extends closer to the euphotic zone, probably is more productive than the deep level bottoms in the major basins of the Strait. There is strong interaction with sediment type here; rocky outcrops appear to support more diverse communities and, ultimately, a higher standing crop of bottom fish than the fine sediments of the basins. The pathways for energy transfers are complex, involving relatively unexplored biological processes such as production by bacterioplankton, fluxes of organic material through pycnoclines of varying intensities, and zooplankton grazing in the deeper parts of the water column.

Integration of data from the foreshore system (Fig. 8) is more difficult; time and space scales are short, leading to unpredictability in physical models. Results tend to be site

TABLE 7. Data on secondary production of zoobenthos from the Strait of Georgia or adjacent Puget Sound.

Species	Location	Production (g ash-free dry $wt \cdot m^{-2} \cdot yr^{-1}$)	Reference
Harpacticus uniremus	Nanaimo Estuary	27	Sibert 1979
Crassostrea gigas ("biodeposits only")	Departure Bay	551	Bernard 1974
Balanus glandula	West Vancouver	449	Wu and Levings 1979
Macoma balthica	Roberts Bank, Fraser Estuary	3	McGreer 1979
Pectinaria californiensis	Deep basin of northern Puget Sound	3−10	Nicols 1975

specific and dependent on local geomorphology, sediment dynamics, wave conditions, and currents (Sibert 1981). The topics of provenance and utilization of detritus have received attention in recent years but it is not yet possible to rate the significance of the various algae and vascular plants involved. The data base for foreshore communities is relatively good and offers many opportunities for syntheses and new research. These ecosystems are complex within a variety of physical settings; they present a great challenge to interdisciplinary research on productivity and systems interactions.

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Pollution in the Strait of Georgia: a Review[1]

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WALDICHUK, M. 1983. Pollution in the Strait of Georgia: a review. Can. J. Fish. Aquat. Sci. 40: 1142–1167.

The Strait of Georgia, when considered as a whole, is still comparatively free of major pollution problems. Local environmental degradation has taken place, however, in waters on the periphery of the Strait, adjacent to urban communities and industries, such as pulp mills. The Fraser River, which is the major source of freshwater to the Strait, introduces natural and man-made materials that can adversely affect its estuary and the marine environment. The Strait of Georgia is flushed regularly, with deep waters being replaced about annually and waters in the upper layer having a considerably shorter residence time. Buildup of pollutants or their effects, e.g. oxygen depletion, are prevented in this way. However, there is refluxing of surface waters into the deep zone from the mixing region at the southern entrance to the Strait, and this means that surface pollutants such as oil could pollute the deep water and be retained there for up to a year. Problems affecting fisheries have been identified at the Fraser River Estuary arising from discharge of sewage treatment plant effluent. The major problem of pollution affecting fisheries in the Strait of Georgia has been bacteriological contamination from sewage, which has necessitated the closure of shellfish beds. The quality of oysters, as represented by condition factor and flavor, has deteriorated in the vicinity of some pulp mills. Evidence so far indicates that the "critical pollutants," e.g. petroleum hydrocarbons, organochlorines, and metals, which are persistent, toxic, and can be bioaccumulated by marine organisms, are present in low concentrations in the water, sediments, and biota away from the Fraser River Estuary. Wood wastes in the Strait of Georgia create a menace to navigation, especially during the spring freshet of the Fraser River.

WALDICHUK, M. 1983. Pollution in the Strait of Georgia: a review. Can. J. Fish. Aquat. Sci. 40: 1142–1167.

Dans l'ensemble, le détroit de Géorgie est encore relativement libre de problèmes majeurs de pollution. Il y eut toutefois dégradation locale du milieu dans les eaux de la périphérie du détroit, au voisinage des communautés urbaines et des industries telles que moulins de pâte à papier. Le fleuve Fraser, la principale source d'eau douce du détroit, apporte des matériaux, tant naturels que résultant d'activités humaines, qui peuvent avoir des effets nuisibles sur l'estuaire et l'environnement marin. L'eau du détroit de Géorgie se renouvelle régulièrement, les eaux profondes étant remplacées à peu près annuellement et les eaux de surface beaucoup plus rapidement. De cette manière, les contaminants ou leurs effets, p. ex. l'épuisement d'oxygène, ne sont pas cumulatifs. Cependant, il y a réintroduction des eaux de surface dans la zone profonde de la région de mélange à l'entrée méridionale du détroit. Cela signifie que les contaminants superficiels, tels que le pétrole, peuvent polluer les eaux profondes et y être emprisonnés durant une période allant jusqu'à un an. On a identifié dans l'estuaire du fleuve Fraser des problèmes affectant les pêches causés par les effluents d'usines de traitement des eaux usées. Dans le détroit de Géorgie, le principal problème de pollution touchant les pêches a été la contamination bactérienne par les égouts, qui a entraîné la fermeture des gisements de mollusques. Dans le voisinage de certains moulins de pâte à papier, la qualité des huîtres, telle qu'indiquée par leur état d'embonpoint et leur saveur, s'est détériorée. Les données recueillies à ce jour montrent que les « contaminants critiques », p. ex. hydrocarbures de pétrole, composés organochlorés et métaux, qui sont persistants, toxiques et susceptibles d'accumulation dans les organismes marins, sont présents en faibles concentrations dans l'eau, les sédiments et les biocénoses loin de l'estuaire du fleuve Fraser.

[1]Based on a paper presented at the Symposium on the Fisheries and Oceanography of the Strait of Georgia, Nanaimo, B.C., February 18–19, 1982.

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Les déchets ligneux dans le détroit de Géorgie présentent un danger pour la navigation, surtout en périodes de crues printannières du fleuve Fraser.

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THE Strait of Georgia (Fig. 1) has always been of interest to man, various Indian tribes having lived along its shores before the white man came, and the European colonizers focusing on it from the time of the earliest explorations by the Spaniards and the British. Captain George Vancouver made perhaps the earliest studies with detailed mapping in the late eighteenth century, when he named the Strait after George III, the reigning monarch of England at the time. Since then, this body of water has been increasingly used by man for transportation, harvesting of living resources, recreation, and waste disposal. After all, it lies between the two major centers of population in the province of British Columbia, Vancouver and the other urban communities of the Lower Mainland to the east and Victoria, Nanaimo, and other Vancouver Island towns to the west. Scientists have studied it quite extensively (Hutchinson and Lucas 1931; Shand 1953; Tully and Dodimead 1957; Waldichuk 1957, 1958a; Parsons et al. 1969; Parsons et al. 1970; Dewey and McMillin 1972; Thomson 1975; Chang et al. 1976; Crean 1976, 1978; Godin et al. 1981; Stronach 1981) to gain a better understanding of the physical, chemical, and biological processes in the Strait. As a marine environment for the valuable fish stocks that are either resident there or utilize this body of water as a nursery area and for feeding during at least part of their life cycle, the various species of Pacific salmon being a prime example, the Strait of Georgia has been of great interest for fisheries scientists.

Although there have been troubled spots along the periphery of the Strait of Georgia, because of urban and industrial input of wastes, pollution has never become a serious problem for the Strait as a whole. This may be so partly by luck rather than by good management. We have never had a major oil spill in the Strait of Georgia. While there are numerous industries along its shores and in the contiguous channels and inlets, and these can cause local pollution, no discharges are such that they create a serious problem for the total waters of the Strait. The same applies to urban wastewater discharges. The worst threat, aside from a large oil spill, could come from the Fraser River, the major source of freshwater to the Strait of Georgia. If it is seriously polluted with toxic, persistent chemicals, it is conceivable that a great deal of damage could be done to sea life that utilizes the Strait. This arises from the fact that the Fraser River water flows over the surface of the seawater in the Strait of Georgia and mixes into the upper layer comparatively slowly until it reaches the southern entrance channels to the Strait. Thus, organisms in the surface layer could be exposed to rather high concentrations of pollutants, owing to the relatively slow dilution of Fraser River water and of any substances contained therein.

The Strait of Georgia, considered in its entirety, is a body of water that is flushed quite regularly by natural circulation and exchange processes. It lacks a shallow threshold sill, common to many inlets and other coastal seas. Hence, replacement of deep water is not impeded substantially by physical barriers and can occur at least annually. In this way, accumulation of contaminants and the effects of some of these on water quality, such as depression of dissolved oxygen concentration, can be avoided. The upper limit of waste input, above which damage due to pollution can occur, is considerably higher in the Strait of Georgia than it would be in a body of water of comparable size where the entrances are constricted both laterally and vertically.

The state of pollution in the Strait of Georgia to 1970 was summarized by Parsons (1972). Because of the interest expressed by the oil industry in exploration for oil in the Strait during the 1960s, along with ongoing explorations off the west coast of Vancouver Island, and because of objections raised by conservationists, a moratorium was placed on any further explorations for petroleum hydrocarbons off the west coast in 1970. The Honourable Jack Davis, Federal Minister of Fisheries and Forestry at the time, proposed that the Strait of Georgia be declared a marine underwater park, and thereby prohibiting any further exploration for oil and gas there. A symposium was even held in October 1970 (Canada Department of Fisheries and Forestry 1970) to further pursue this possibility, and several distinguished international celebrities, including Commandant Jacques Yves Cousteau, were invited to speak. As I recall, the main cause for concern expressed by Commandant Cousteau was the large volume of silt being introduced into the Strait of Georgia by the Fraser River; this reduces light penetration and underwater visibility. He felt that the first remedial measure should be removal of this silt. At about that time, B.C. Hydro was considering a project, Moran Dam, that could have at least partly fulfilled this objective. There were other obstacles to making an underwater park in the Strait of Georgia noted at this symposium, such as industries, maritime transportation, and commercial fishing. Nevertheless, the Honourable Jack Davis felt that this matter should be pursued further and an Interdepartmental Marine Park Task Force was established. The Technical Working Group for this Task Force worked quite diligently on this subject during 1971–72 and prepared a well-balanced and informative report. Because of some sensitivity, it was marked "Confidential" and received rather limited circulation and attention.

Another report that was marked "Confidential" (later "For Government Use Only"), and as a result seen by few people, was the "Report of the Task Force on the Environmental Problems of the Lower Fraser and Strait of Georgia," issued in three volumes in July 1971. Representing seven federal departments and agencies having environmental responsibilities, this task force was charged with identifying environmental problems in the lower Fraser River and the Strait of Georgia and recommending initiatives in the area. Unfortunately, the report had little impact in that it failed in its major objective of stimulating a federal–provincial study agreement for the lower Fraser River and Strait of Georgia under the Canada Water Act. Partly for this reason and partly because

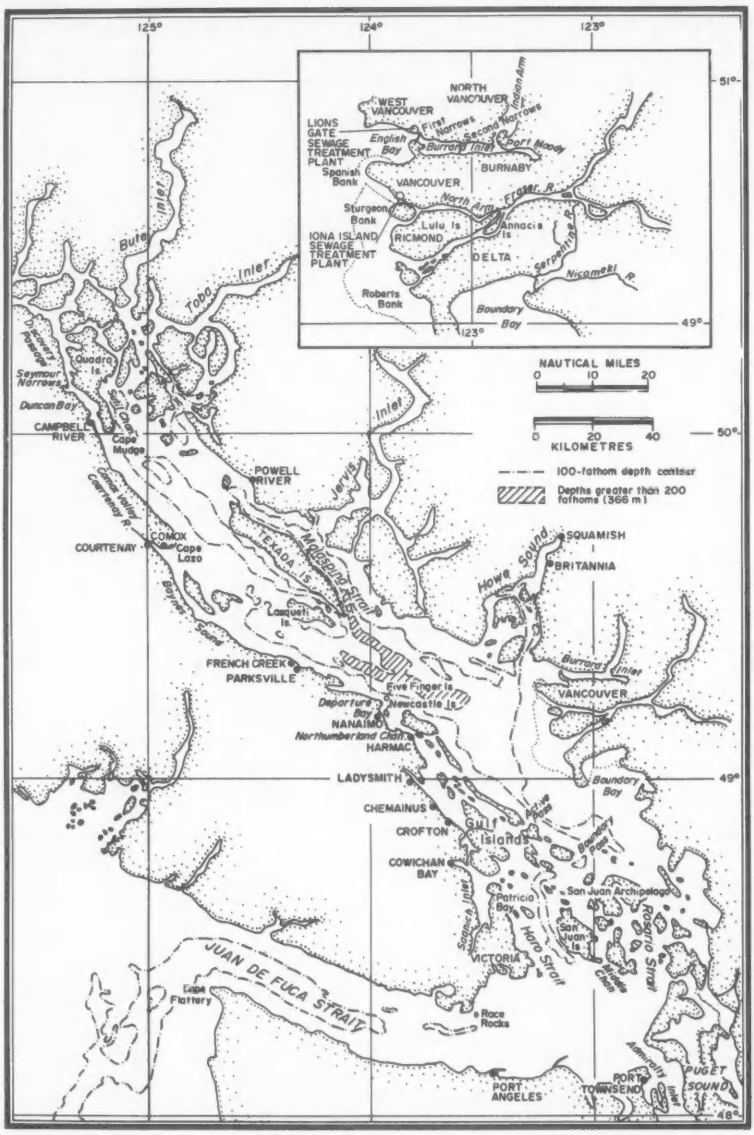

FIG. 1. Basic topographical features of the Strait of Georgia. Inset: Fraser River Estuary and Vancouver area.

the proposed Strait of Georgia Program under the Fisheries and Marine Service Pacific Region was never funded by Treasury Board, no major large-scale investigations on either living resources or environmental quality in the Strait of Georgia have been undertaken during the last decade. This review, therefore, is based largely on individual studies on certain aspects of water quality in the Strait of Georgia; a full picture of the state of pollution cannot be provided. Perhaps some of the gaps in knowledge can be identified for future investigation in order that protection of the water quality in

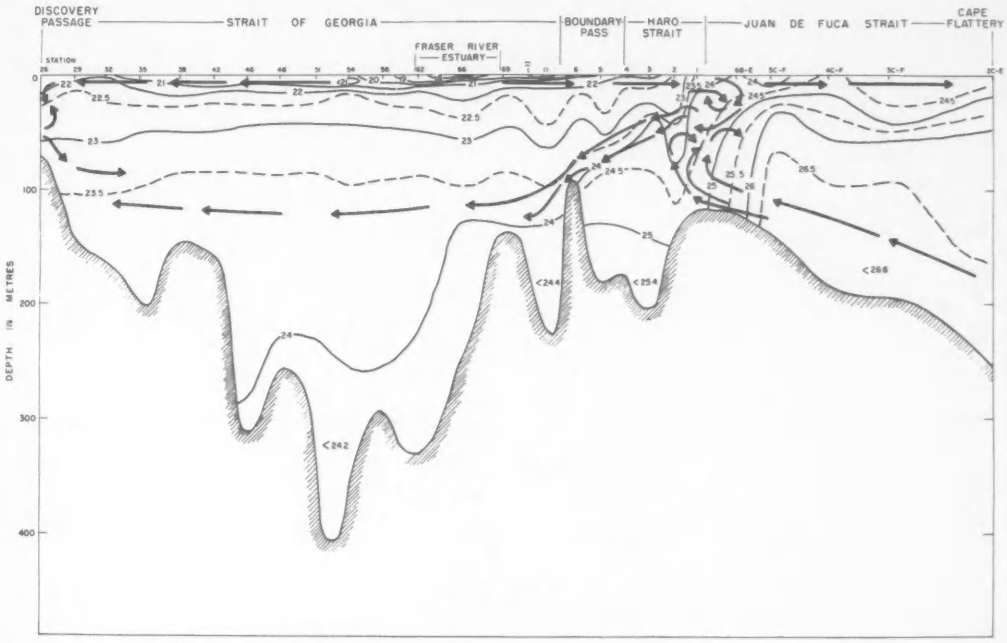

FIG. 2. Longitudinal section of density (σ_t) distribution through the Strait of Georgia–Juan de Fuca Strait system and general movement of water during September 1952. (From Waldichuk 1957)

the Strait can be assured in the event of new major industrial developments.

Flushing Rate of the Strait of Georgia

The physical behavior of a marine system determines to a large extent the degree of pollution in that system under a given amount of waste input (Waldichuk 1968). It is not within the scope of this review to fully discuss the physical oceanography of the Strait of Georgia, which will be exhaustively covered by another paper in this symposium (LeBlond 1983). However, it is essential to at least partly set the stage with the important concept of water exchange in the Strait of Georgia. The rate with which a body of water is replaced is extremely crucial in establishing the extent of pollution that exists in that body of water. If the residence time for the deep water in a given basin is many years, which often occurs in stratified systems with shallow threshold sills, then one can expect that a high degree of pollution will result if there is a substantial waste input.

The Strait of Georgia has a relatively free connection with the open ocean through Boundary Pass, Haro Strait, and Juan de Fuca Strait (Waldichuk 1957). Moreover, there is a zone of intensive vertical mixing in the channels from Boundary Pass to Juan de Fuca Strait, as shown in Fig. 2. The intermediate and deep waters in the Strait of Georgia undergo replacement whenever their density is exceeded by that of the mixture at the southern end of the Strait. The most effective period for such replacement occurs during the late summer and autumn, when the Fraser River discharge is low and upwelling off the west coast of Vancouver Island has contributed dense water of high salinity and low temperature to Juan de Fuca Strait and the mixing zone in the San Juan Island area. Although the rate of replacement has not been fully evaluated over the course of a number of years, the data examined for the period from 1949–53 suggest an annual replacement of the deep waters. The dissolved oxygen concentrations in the deep water during September 1952 (Fig. 3) do not suggest that the water has been present there for longer than a year.

A point that should be noted here is that a certain proportion of the surface water is refluxed through the system as a result of the mixing zone at the southern entrance to the Strait of Georgia. Any material, such as oil, mixed into the water column in the Boundary Pass area can find its way into the deep zone of the Strait. If sedimentation processes cause such pollutants to enter the sediments, or if there is uptake by benthic marine organisms, then accumulation of the material could occur.

The movement of any substances introduced into the surface water of the Strait of Georgia, provided it is conservative in nature, can be predicted to some extent from the behavior of freshwater. The amount of freshwater in the upper layer of the Strait was evaluated for 1950 (Waldichuk 1957) and compared with the river discharge (Fig. 4). The peaks are

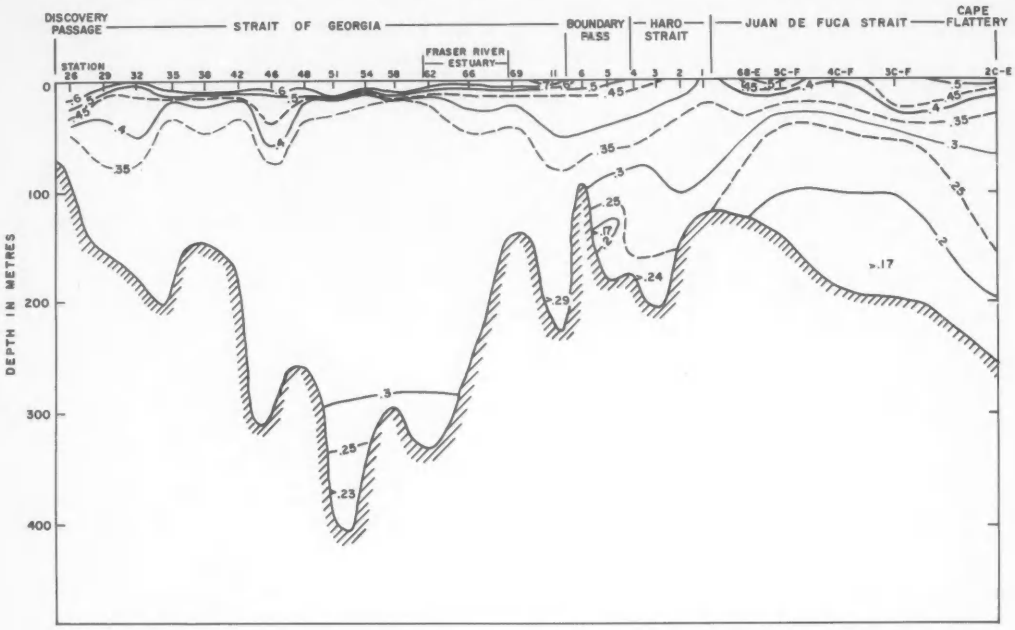

FIG. 3. Longitudinal section of dissolved oxygen distribution in (milligram-atoms per litre) through the Strait of Georgia–Juan de Fuca Strait system during September 1952. To convert milligram-atoms per litre to milligrams per litre, multiply by 16. (From Waldichuk 1957)

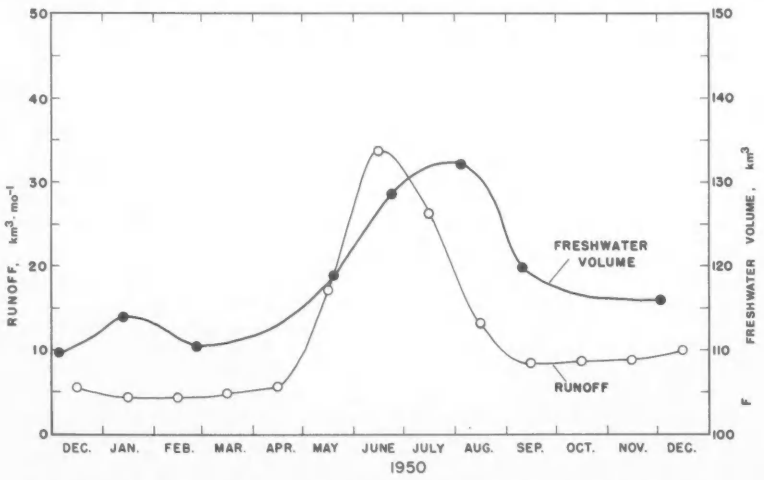

FIG. 4. Seasonal variation of the amount of freshwater in the upper layer of the Strait of Georgia in relation to total runoff during 1950. (From Waldichuk 1957)

approximately 1 mo apart, indicating that it takes about that length of time to reach an equilibrium in the surface layer of the Strait of Georgia in response to the freshwater inflow. This suggests that the flushing rate of the upper layer in the Strait of Georgia could be fairly rapid.

Another way of looking at the freshwater budget in the

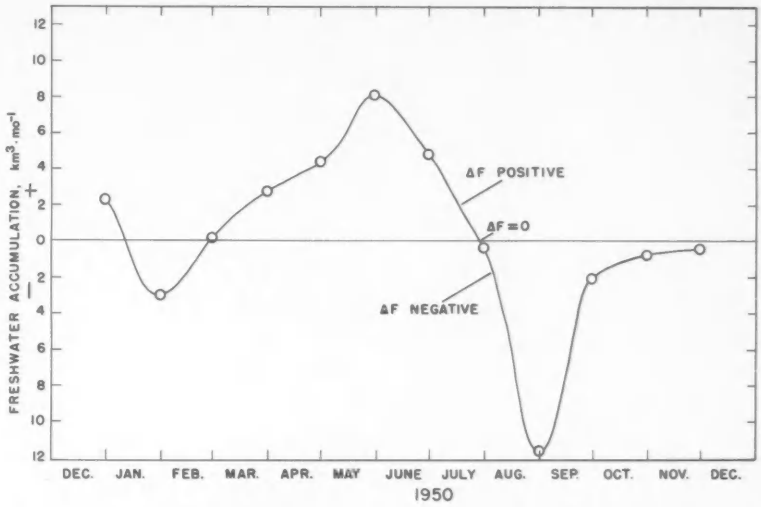

FIG. 5. Seasonal variation in monthly change in freshwater volume (ΔF) in the Strait of Georgia during 1950. (From Waldichuk 1956)

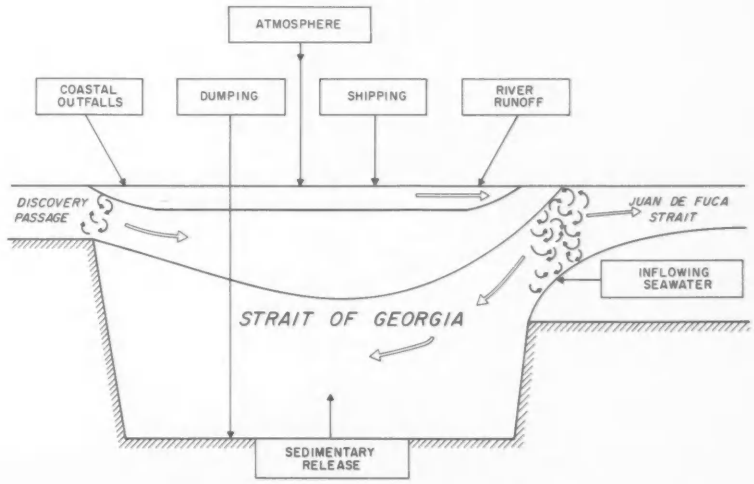

FIG. 6. Sources and pathways of contaminants entering the Strait of Georgia.

Strait of Georgia and the way that the system responds to freshwater input is through the monthly change of volume of freshwater, ΔF, in the Strait (Waldichuk 1956) (Fig. 5). When $\Delta F = 0$, just before the beginning of August, the outflow of freshwater is equivalent to the inflow. Then the outflow exceeds the inflow (ΔF is negative) until the beginning of September, after which the outflow begins to approach the inflow again.

A simple expression for residence time of freshwater is the quotient of the freshwater volume, V_F, in the Strait divided by the rate of input, I. If the average volume of freshwater in the Strait of Georgia is accepted as 123 km^3 (Waldichuk 1957), then V_F/I is equal to about 0.8 yr or 9.6 mo. The actual residence time of the upper layer of water in the Strait of Georgia is probably somewhat shorter.

More precise evaluation of the flushing rate in the Strait of Georgia and year-to-year variation should be carried out on a more extensive set of oceanographic data.

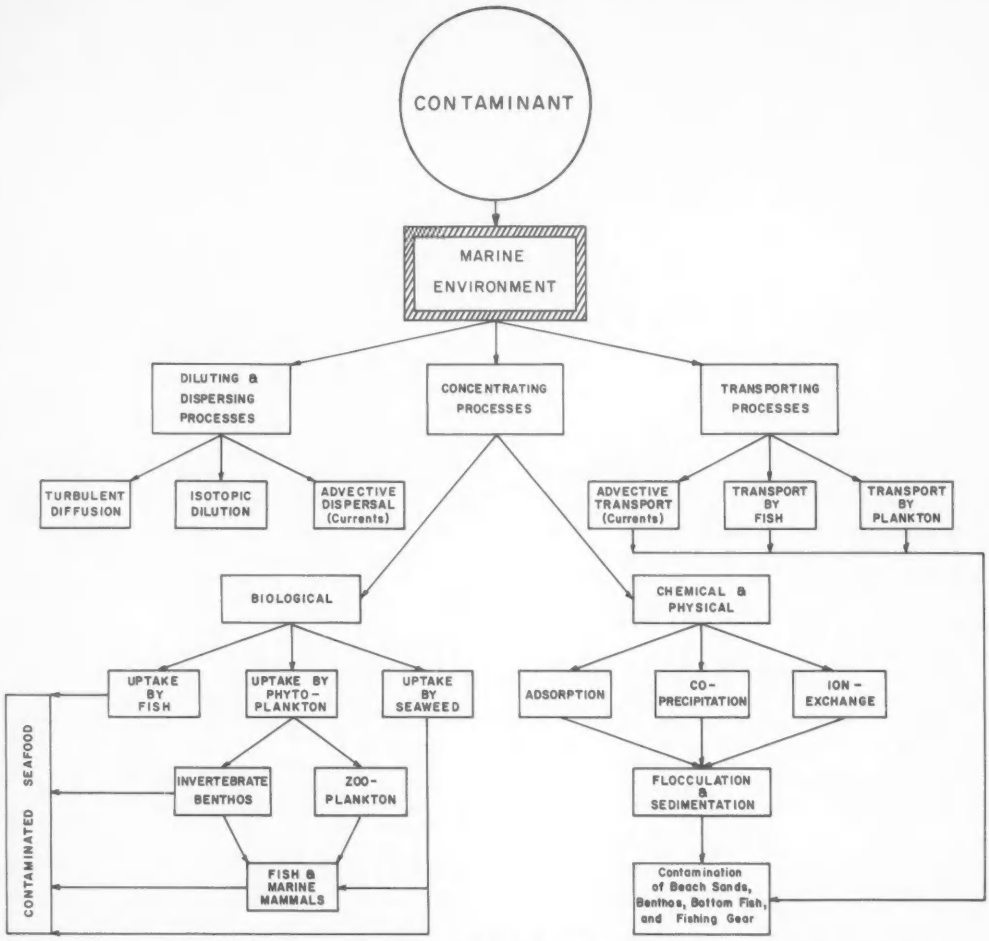

FIG. 7. Schematic diagram showing the fate of a contaminant in the marine environment, especially as it relates to an estuary.

Routes of Entry of Contaminants

There is a variety of ways by which contaminants can enter the Strait of Georgia. Some of the more obvious routes may not be the mode by which the largest proportion of the contaminants enters the sea. Certain pathways hitherto considered as only incidental are gaining recognition. However, estimates have not been made of the proportion of each contaminant that enters the Strait of Georgia by any given pathway, and one can only speculate about the relative importance of different pathways. A schematic illustration of different contaminant input pathways is shown in Fig. 6.

RIVERS AND RUNOFF

Depending on the drainage basin and the types and quantities of wastes received, rivers may be an extremely important route for entry of contaminants into the sea. By far the greatest proportion (80%) of freshwater entering the Strait of Georgia comes from the Fraser River. With it may come also the largest volume of contaminants that could potentially affect the water quality of the Strait. Industries and urban communities along the Fraser River contribute a certain amount of industrial effluent, domestic sewage, and urban runoff to its waters. These wastewaters and drainage effluents become somewhat modified during the course of their stay in the river.

As the waterborne wastes enter the estuary, a number of biogeochemical processes, such as flocculation, coprecipitation, sorption, gravitational settling, and biological uptake, tend to fix the contaminants in the estuarine sediments or in

the biota. What proportion of a given constituent becomes removed from Fraser River water and deposited in the sediments of the estuary depends on a number of factors, e.g. chemical characteristics of the constituent, suspended load, and rate of discharge of the Fraser River. Certain metals, especially if they are present in the particulate form, may be almost totally removed from the water and deposited in the sediments. Dissolved constituents have a greater chance than suspended solids of actually entering the sea, unless they become coprecipitated or adsorbed onto particulate matter and are settled out into the sediments. Studies on the exchange of metals between the water and sediments in the Fraser River Estuary have been underway for some time (Thomas and Grill 1977; Fletcher et al. 1983). The fate of a pollutant in the estuary is shown schematically in Fig. 7.

Outfalls

Wastewaters discharged directly into the Strait of Georgia through outfalls may undergo a number of processes similar to those encountered in estuaries. It depends to some extent on the design of the outfall and the characteristics of the receiving waters in the area as to what eventually happens to the pollutants in the discharged effluents. A deep discharge pipe with diffuser ports leads to a rapid dilution and dispersion of the effluent. Solid particles will settle near the outfall by gravitation, while dissolved constituents usually become diluted and dispersed by mixing and currents. Dissolved and suspended organic constituents may undergo decomposition through the action of bacteria, leading to oxygen uptake from the receiving waters and a possible oxygen deficiency in these waters. Bacteria from sewage, if it is not disinfected, may not only contaminate the water but also the marine organisms if they are filter feeders, such as many species of molluscan shellfish. For this reason, oyster-growing grounds near shallow (<10 m) domestic sewer outfalls may be closed or restricted for oyster harvesting commercially along the shoreline of the Strait of Georgia. This is less likely to happen with outfalls more than 50 m deep, unless the volume of raw sewage discharged is very large.

Surface or shallow outfalls affect the character of the bottom sediments in the vicinity of the sewage discharge. This is strikingly exemplified by conditions in the vicinity of the effluent trench from the Iona Island Sewage Treatment Plant. Organic substances have heavily contaminated the sediments along the trench. The substrate has been adversely affected for colonization by bottom organisms, and the water overlying the sediments sometimes becomes severely depleted of dissolved oxygen. Less acute situations prevail in areas, such as the former shallow sewage outfall for Nanaimo, at the north end of Newcastle Island. A surface sewage plume was almost always visible, which made it particularly unattractive for bathing in the vicinity. On the other hand, sewage discharge into the swift, turbulent waters of the First Narrows in Burrard Inlet from the Lions Gate Sewage Treatment Plant in West Vancouver exhibits little surface evidence of sewage.

Ocean Dumping

Ocean dumping has been practised for some time in the Strait of Georgia at a number of selected dumpsites. This practice is now quite closely controlled under the Ocean Dumping Control Act, which came into effect in 1975. There are two major dumpsites in the Strait of Georgia that serve the lower mainland of British Columbia: (1) Point Grey dumpsite, which is used for disposal of dredge spoils from Vancouver Harbour and the North Arm of the Fraser River, and (2) the Sand Heads dumpsite for dredge spoils from the main channel of the Fraser River. Other sites in the Strait of Georgia used less frequently include the Five Finger Islands dumpsite off Nanaimo, the Cape Lazo dumpsite for Courtenay–Comox, Cape Mudge dumpsite for Campbell River and Duncan Bay, and the Malaspina Strait dumpsite for Powell River. Figure 8 shows the major dumpsites, both historical and those currently being used.

Most of the material dumped at these sites consists of gravel, sand, silt, and mud, sometimes contaminated with wood wastes and metals. Its main effect, of course, is the alteration of the bottom characteristics in the dumping area. It may affect spawning grounds for such species as Pacific cod (*Gadus macrocephalus*) and lingcod (*Ophiodon elongatus*). Certain substances leached from the dumped material may be toxic to or bioaccumulated by bottom organisms. For this reason, regulations under the Ocean Dumping Control Act prohibit the dumping at sea of dredge spoils or other such materials when so-called Schedule I substances (e.g. mercury, cadmium, organohalogens, oils, persistent plastics) exceed certain concentrations. There are a few cases requiring the ocean dumping by barge or other vessel of industrial wastes or surplus chemicals. In the very few instances when such dumping was required, e.g. the disposal of barite from a drill ship, this was done offshore under carefully controlled conditions of discharge and dispersal.

Shipping

Another source of direct input of contaminants into the sea is ships. This may consist of ship-generated sewage and garbage and deliberate or accidental release of cargo. At one time, sewage and garbage were routinely discharged into the Strait of Georgia by all vessels plying these waters. Under Section XX of the Canada Shipping Act this is now quite closely controlled for larger vessels by Transport Canada. Holding tanks or shipboard sewage treatment systems are generally used by ferries and merchant ships. Fishing boats and recreational vessels are still largely uncontrolled for sewage disposal but usually practise self-discipline in avoiding garbage disposal at sea. Sewage from such vessels has been of some concern in oyster-growing areas (B. Kay, Environmental Protection Service, West Vancouver, B.C., unpublished data).

The loss of cargo in collisions, groundings, and other shipping mishaps can be a source of pollution in the Strait of Georgia, as well as anywhere else where there is marine transport of materials. Fortunately, this has not been commonplace in the Strait. Oil tankers often wash out their tanks and discharge the washings into the sea after unloading a shipment of oil. But this is prohibited in the Strait of Georgia under the Canada Shipping Act. There is occasional accidental spillage from both tankers and shore facilities, resulting

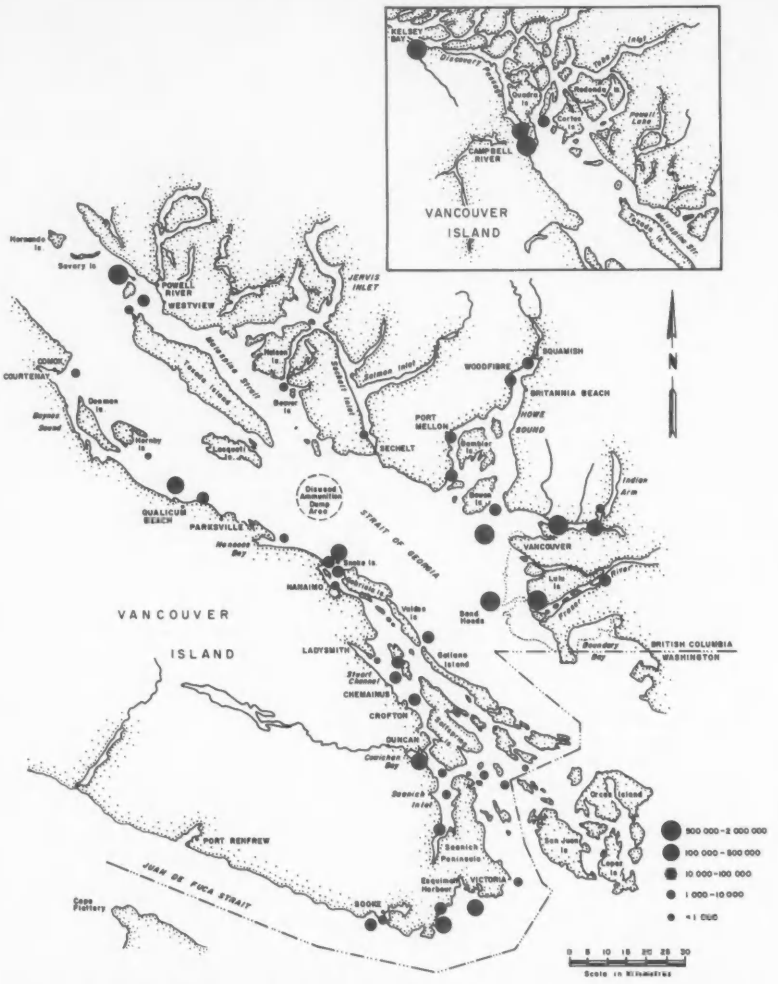

FIG. 8. Location of the principal existing and historical dumpsites in the Strait of Georgia, with volumes of materials dumped in cubic metres to 1980. Inset: northern Strait of Georgia and contiguous channels. (From Ward and Sullivan 1980)

in oil seepage into the Strait. With contingency measures in place, there is close control on spillage and spread of oil from shipping accidents by the Coast Guard and from shore facilities by the Environmental Protection Service.

INFLOWING SEAWATER

An often ignored or neglected source of materials into the Strait of Georgia is the inflowing seawater. The seaward movement of freshwater through the Strait and removal of seawater by entrainment into the upper brackish layer ensures that there is a continuous inflow of seawater to replace that which is removed. This inflowing seawater may contain substances above background levels, derived elsewhere, which could be a source of pollution in the Strait of Georgia. In mass balance calculations of nutrients in the Strait, for example, it is essential to take into account the quantities introduced by inflowing seawater, which may be derived from upwelled seawater off the west coast of Vancouver Island. But there may also be pollutants introduced from tanker catastrophes or from industrial discharges in other parts of the Strait of Georgia–Juan de Fuca Strait system. For example, con-

taminants from industries in Puget Sound can reach the deeper zones of the Strait of Georgia through the vertical mixing that takes place in Admiralty Inlet, at the entrance to Puget Sound, and in the San Juan Channels, at the southern entrance to the Strait of Georgia, and then by the penetration of this mixed water into the intermediate and deep zones of the Strait of Georgia.

Sediments

Materials deposited in the sediments are not necessarily fixed there forever. These materials may become mobilized by a number of natural processes and man-made activities. Certain metals may be released from the sediments, for example, by the process of diagenesis, which is the sum of all biogeochemical interactions taking place within the sediments. Disturbance of sediments in estuaries by accelerated inflow of freshwater during freshets can lead to desorption of metals from the sedimentary particles, as noted in the Fraser River Estuary (Thomas and Grill 1977). Dredging of sediments can mobilize metals, as the sedimentary particles that may have been in an anoxic, reducing environment are suddenly exposed to oxic conditions.

While sediments probably make only a small contribution to the mass balance of contaminants in the Strait of Georgia, this source must be borne in mind when a rigorous analysis is carried out.

Atmosphere

Increasing recognition is being given to the role the atmosphere plays in transporting contaminants from the source to various bodies of water. Its role in transporting sulfur dioxide and oxides of nitrogen to freshwater bodies, with a net result of acidification of lakes and streams, is now well known. Other substances, such as DDT and PCBs, are transported worldwide by air currents and washed out by rain into freshwater and marine environments.

Virtually nothing is known about the magnitude of the contribution of contaminants by the atmospheric pathway to the Strait of Georgia. It can be anticipated, however, that certain metals and petroleum hydrocarbons enter the Strait of Georgia by this route. Lead from combustion of leaded gasolines in automotive vehicles must certainly find its way into the Strait of Georgia through the atmosphere. Prevailing winds are an important factor in the extent to which the atmosphere conveys combustion products into the Strait. In this regard, southeast winds may be the carrier for contaminants emitted by industry and automotive vehicles in the urban centers of Seattle and Tacoma in Washington State, with some rainout into the Strait of Georgia.

Sources and Effects of Marine Pollution

In the previous section, the different routes by which contaminants enter the Strait of Georgia were reviewed. It is proposed to review here the different sources of the various contaminants and to discuss some of the pollution problems that they create. The sources can be divided broadly into domestic sewage and industrial wastes. But there are numerous effluents entering the Strait of Georgia that cannot be classified under the foregoing two categories, so that it is probably preferable to subdivide the effluents into urban and industrial.

Municipal Wastewaters and Urban Runoff

Effluents from urban communities can be roughly subdivided into domestic or sanitary sewage (or wastewaters) and surface drainage, which consists of runoff from the streets during and following a rainfall or thawing of ice and snow. While the discharge of sanitary sewage remains relatively constant, the discharge of drainage waters can vary from zero during dry periods to a large surge under storm conditions. In communities where storm sewers are combined with sanitary sewers, serious problems can be encountered in any sewage treatment facilities during heavy runoff.

Domestic sewage — The population along the Strait of Georgia is concentrated on the lower mainland of the province in the Vancouver area. Whereas raw sewage was discharged into the lower Fraser River and the sea through assorted outfalls 30 yr ago, the Greater Vancouver Sewerage and Drainage District has been following essentially the plan outlined in the Rawn Report (Rawn et al. 1953) for integrating the sewerage system in the Greater Vancouver area and consolidating the discharges through treatment plants at a few selected points. The Iona Island Sewage Treatment Plant was the first of these to go into operation. It was opened in 1963 to serve mainly Metropolitan Vancouver. The plant provides primary treatment, to remove the solids, and disinfection by chlorination when the coliform level in waters on the Spanish Banks becomes too high. The effluent is discharged through an open ditch onto Sturgeon Bank, with a jetty on the north side of the ditch to prevent the effluent from flowing directly onto the recreational beaches in English Bay. At present, a study is underway considering the disposal of this effluent through a deep outfall with a diffuser, in order to halt the kinds of ecological problems encountered near the existing outfall.

The Iona Island Sewage Treatment Plant was soon followed by the Lions Gate Sewage Treatment Plant, just west of the northern end of the Lions Gate Bridge, to serve the municipalities on the north shore of Burrard Inlet. Primary treatment providing solids removal is accorded the sewage in this plant, with effluent being discharged by one pipeline and sewage sludge by another at a depth of 12 m into the First Narrows. In more recent years, primary treatment plants have been installed on the lower Fraser River at Lulu Island and Annacis Island to serve the surrounding urban municipalities in this part of the Fraser River Delta. The effluents are discharged through pipelines with diffusers to the deepest parts of the Fraser River.

The story of sewerage installations, treatment plants, and submarine outfalls can be repeated on a smaller scale for many of the other cities and towns bordering the Strait of Georgia. These include Nanaimo, Courtenay, Comox, Parksville, Chemainus, and Ladysmith. Courtenay is served by a sewage lagoon rather than a treatment plant at present, but planning is underway for a treatment plant and a deep outfall off Cape

Lazo to serve Comox and Courtenay. Septic tanks are still common in rural and suburban areas. Seepage from malfunctioning septic tank systems eventually drains into the sea and, in some coastal marine areas, contributes to high coliform counts.

Basically, sewage contributes to five types of pollution problems: (1) bacteriological–viral contamination, (2) biochemical oxygen demand, (3) organic solids deposition, (4) nutrient enrichment, and (5) other chemical contamination. In the Strait of Georgia, the main problem that has arisen so far from sewage discharge, through affecting living resources, has been bacteriological–viral contamination of water over shellfish beds. This has led to closure or restriction (depuration required prior to marketing) for harvesting by regulatory agencies in certain shellfish areas. Biochemical oxygen demand has led to acute oxygen deficiency in the area of the Iona Island Sewage Treatment Plant outfall, where mortality of fishes has been observed (I. K. Birtwell, West Vancouver Laboratory, West Vancouver, B.C. unpublished data), and the intertidal benthos has been altered owing to modification in substrate and low dissolved oxygen (Otte and Levings 1975). In general, such effects would not be expected, even with a large volume of effluent, if it were discharged through a deep diffuser. Nutrient enrichment has not yet been identified as causing eutrophication problems in the Strait of Georgia, although increased nutrient levels and higher primary productivity during the last decade at a number of stations have been suggested (Stockner et al. 1979). There has been some debate about whether eutrophication in the Strait of Georgia as a result of sewage input has actually occurred so far or whether the differences in productivity observed during the 1960s and 1970s are due to natural causes or to changes in measurement methodology (Parsons et al. 1980; Clark and Drinnan 1980; Stockner et al. 1980). It is conceivable that high nutrient loading from sewage could lead to excessive algal production in poorly flushed, semi-enclosed embayments. Increased phytoplankton productivity at the periphery of the Fraser River plume could be a product of elevated levels of nutrients in Fraser River water due to larger input of sewage and other nutrient-rich effluents.

Chlorination of sewage can lead to a host of organochlorine compounds in the effluent, which are not only toxic but are also capable of being bioaccumulated by marine organisms. The presence of a number of these compounds has been identified in both the receiving waters and in starry flounders, *Platichthys stellatus*, in the vicinity of the Iona outfall at the West Vancouver Laboratory (I. H. Rogers, West Vancouver Laboratory, West Vancouver, B.C., personal communication). The seriousness of this contamination has not yet been established.

A problem that arises from discharge of municipal wastewaters is the entry of assorted chemicals and industrial wastes into the sewer system from small industries, laboratories, hospitals, dental clinics, and other operations. These substances are often not amenable to treatment and may interfere with the normal operation of a treatment plant. Such industrial and institutional wastes are frequently the source of metals and petroleum hydrocarbons in sewage and probably result in the high metal levels found in sediments and marine organisms near sewer outfalls (Grieve and Fletcher 1976; Parsons et al. 1973). More costly advanced treatment technology is required to remove these "foreign" materials from sewage, or it is necessary to control them at source, if the effluent from a sewage treatment plant must be free of such materials. These are the alternatives being faced at the Iona Island and Annacis Island sewage treatment plants.

Urban runoff — Increasing recognition is being given to the problems created by urban runoff. A great deal of organic and inorganic material is washed off city streets by a heavy rainfall. The first storm after a dry period ("first flush") is especially important for flushing away materials accumulated on streets, sidewalks, and building rooftops. Such substances as lead and petroleum hydrocarbons may be present in storm-sewer water, resulting from spills and leaks from automotive vehicles and from condensation and rain washout of combustion products of gasoline. Used crankcase oil, enriched in polyaromatic hydrocarbons, has been considered to be a potential mutagenic burden among various petroleum hydrocarbons entering inland, estuarine, and other coastal waters (Payne et al. 1978). Pesticides used for controlling weeds and insects on lawns, garden plots, boulevards, and parks may also be present. Excrement from animal pets and birds is always present in the urban environment, and this contributes to the high coliform count in storm runoff. Salt arises from wintertime municipal deicing and snow-removal activities. There is always an abundance of inorganic and organic particulate material in urban runoff, and this material usually settles out near the outfall.

Industrial Wastes

The industrial wastes entering the Strait of Georgia arise from a number of individual large plants on the perimeter of the Strait and in its contiguous channels and tributary inlets, as well as from assorted smaller plants in the urban communities. The environmental effects of waste discharges from point sources, such as the isolated individual large plants, can be more easily assessed than those arising from collective discharges of numerous industries or from such non-point sources as agricultural runoff. An attempt is made here to enumerate the different industrial sources of wastes entering the Strait of Georgia and to qualitatively note the ecological effects that can be produced.

Pulp and paper mills — Two pulp mills, one at Powell River and the other at Harmac, Nanaimo, discharge their effluents directly into the Strait of Georgia (Fig. 9, inset). Four pulp and paper mills, located at Crofton, Port Mellon, Woodfibre, and Duncan Bay, near Campbell River, discharge effluents into contiguous channels or a tributary inlet. All these mills produce kraft pulp and newsprint. They discharge their effluent, generally untreated, directly into the sea through deep outfalls with diffusers at two of the mills and through shallow outfalls at the others. Deep outfalls are being planned for at least two of the other mills. In addition to the coastal pulp and paper mills, there are several interior mills discharging effluents into the Fraser River or its tributaries (three at Prince George, one at Quesnel, and one at Kamloops). Effluents from small paper-producing mills

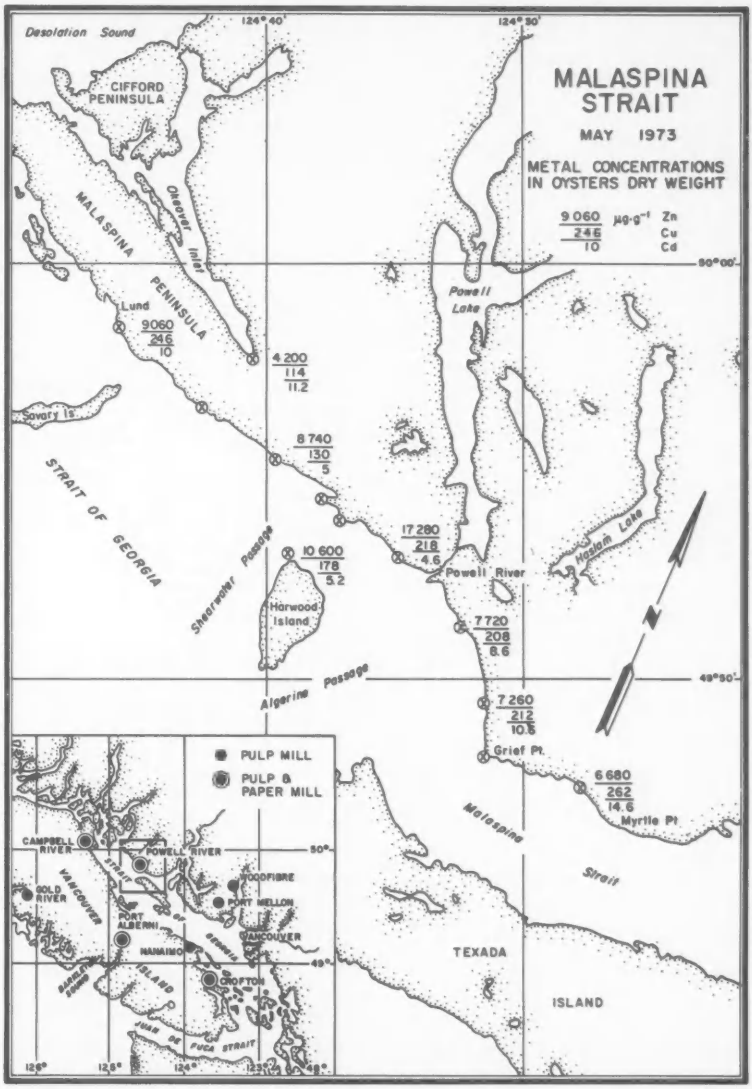

FIG. 9. Zinc, copper, and cadmium concentrations in oysters at various locations along the eastern shores of the Strait of Georgia prior to discontinuation of zinc dithionite as a brightening agent at the Powell River pulp and paper mill. (From Waldichuk 1974)

on the lower Fraser River, located at New Westminster and Annacis Island, add to the large volumes of pulp and paper mill effluents discharged to the river farther upstream. All interior mills have settling ponds and biobasins for primary and secondary treatment of their effluents, so that suspended wood solids are removed, and the toxicity and biochemical oxygen demand (BOD) of the effluent are substantially diminished.

Kraft pulp and paper mill effluents contribute mainly to three types of ecological problems: (1) toxicity, (2) BOD, and (3) settleable wood solids. Toxicity arises from the toxic constituents in any of the "black liquor" that may escape with

the pulp wash waters and in bleach-plant effluents from caustic extraction and chlorination. Toxicity, of course, is highest near the outfalls and rapidly diminishes as the effluent undergoes dispersion and dilution. The acute toxicity for the full-bleach kraft mill effluent from the Harmac pulp mill, obtained in seawater bioassays in the mid-1950s using sockeye salmon (*Oncorhynchus nerka*) underyearlings as test organisms, was such that 4.8% of the total effluent in seawater of 20‰ salinity and 17.8°C was the limiting concentration for mortality, below which survival was complete and independent of exposure time (Alderdice and Brett 1957). Since then, there have been many improvements in recovery and treatment of kraft mill effluent, so that its acute toxicity has been considerably reduced. However, it has been recognized that kraft mill effluent can exert a sublethal stress at considerably lower concentrations than that causing mortality in fish. Sublethal effects have been recognized at 0.02–0.05 of the LC50 (concentration at which 50% of the test organisms die during a given period of exposure) (Davis 1976; Walden 1976).

The BOD of kraft mill effluent has been decreasing with improvements in recovery and treatment within the mills. At one time (mid-1950s), the 5-d BOD of the full-bleached kraft mill effluent from the Harmac mill was 97 $mg \cdot L^{-1}$ (Greer et al. 1956). This amounted to a total daily oxygen demand of 1.8×10^4 $kg \cdot d^{-1}$ to stabilize the effluent from a 500-$t \cdot d^{-1}$ mill. While such a level of oxygen demand has caused problems in poorly flushed bodies of water, such as Alberni Inlet, there has been no evidence of serious oxygen deficiency in waters receiving pulpmill effluents around the Strait of Georgia. With the trends toward better recovery of organic substances in mills and disposal of effluent through submarine diffusers, providing rapid dispersion and dilution, it is not anticipated that there will ever be a severe problem of oxygen deficiency due to pulpmill effluents in receiving waters of the Strait of Georgia, even if there were major expansions of existing mills. Any new mills, of course, are required by regulations to meet stringent measures to avoid any kinds of pollution problems, including oxygen deficiency in receiving waters.

Settleable wood solids can create problems in the vicinity of pulp mills. They may accumulate in sludge banks near outfalls and blanket the bottom of substantial areas (Werner 1965; Werner and Hyslop 1968a), causing undesirable changes in bottom substrates. Decomposition of these wood wastes can reduce the dissolved oxygen not only in the sediments but also in the overlying water. Gases may evolve from some of these accumulations of wood solids in advanced stages of decomposition, when anaerobic conditions prevail (Werner and Hyslop 1968b). The increasing recovery of wood solids from pulpmill effluents, to meet provincial and federal regulations, has ensured that the discharge of these materials into receiving waters is being controlled at the lowest practical level attainable with existing technology.

Pulpmill effluents in the past contained certain persistent chemicals, such as mercury and zinc, that could lead to problems of bioaccumulation to high concentrations by marine organisms. Mercury-based organic chemicals were used at one time as effective slimicides in pulp and paper mills. They were voluntarily discontinued by the pulp and paper industry of British Columbia around 1960 because of a requirement of the U.S. Food and Drug Administration that there be zero mercury concentration in paper used for food wrapping. However, a certain amount of residual mercury remained in the sediments near pulp and paper mill outfalls, and now these deposits pose a problem in some instances in which dredging is required and the dredge spoils must be dumped at sea under regulations of the Ocean Dumping Control Act.

Zinc dithionite (referred to as zinc hydrosulfite in the industry) was routinely used for brightening newsprint at one time in British Columbia mills. It was found in the early 1970s that zinc was accumulating to high concentrations in oysters near pulp and paper mills where zinc dithionite was employed (Fig. 9) (Waldichuk 1974; Ellis et al. 1981). The industry took the initiative to change the brightening agent from zinc dithionite to sodium dithionite in 1973.

We are finding higher-than-background concentrations (>1 $\mu g \cdot g^{-1}$) of cadmium in sediments near pulpmill outfalls. Its source is unknown, but high cadmium concentrations are typical of sediments in the vicinity of various industrial operations, e.g. shipyards, along the Vancouver waterfront. Being one of the prohibited substances under the Ocean Dumping Control Act, cadmium poses problems when it exceeds 0.6 $\mu g \cdot kg^{-1}$ in the solid phase of sediments, if ocean disposal of dredge spoils from these areas is proposed.

Problems of pulpmill effluent disposal into the sea in British Columbia, including those arising from mills located on or adjacent to the Strait of Georgia, have been reviewed (Waldichuk 1962). Dispersion of effluent from a diffuser at the Crofton pulp mill has been described (Waldichuk 1964), and the flushing rates and oxygen balance in Northumberland Channel receiving effluent from the Harmac pulp mill have been evaluated (Waldichuk 1965a). The trend is toward deep outfalls with diffusers at all coastal mills. Solids recovery in settling ponds or in clarifiers is sometimes practised, but secondary treatment of effluent at these mills is uncommon.

Chloralkali plants — There are three chloralkali plants along the shores of the Strait of Georgia or in its tributary inlets: (1) North Vancouver on Burrard Inlet, (2) Harmac near Nanaimo on Northumberland Channel, and (3) Squamish in Howe Sound. They produce chlorine and caustic (sodium hydroxide), which are mainly utilized for bleaching purposes by the pulp and paper industry of British Columbia. Effluents from chloralkali plants can be toxic, and there are records of fish kills during the 1960s in the vicinity of the plant at Harmac, Nanaimo. Highly toxic chemical residues were released when concentrations of fish were present in Northumberland Channel and the tidal conditions were unfavorable for rapid dispersion and dilution of the released chemicals.

The main long-term problem with chloralkali plants arises, however, when the mercury cell system is used in production. The plants at Nanaimo and North Vancouver have the Hooker diaphragm cell, which causes no known pollution problem in itself, but the plant in Squamish employs the mercury cell for production of chlorine and caustic by electrolysis of brine. Mercury from the cell was found to be entering the sea and contaminating sediments and marine organisms in the upper end of Howe Sound (Thompson and McComas 1973;

Macdonald and Wong 1977; Harbo and Birtwell 1978). The federal Minister of Fisheries and Forestry issued a decree in 1970 that all chloralkali plants in Canada using the mercury cell must reduce their mercury losses, and regulations promulgated shortly thereafter limit these losses to 0.0025 kg·t chlorine^{-1} produced. The FMC Chemicals Ltd. plant in Squamish installed a holding pond for their effluent, which virtually eliminated the discharge of mercury to Howe Sound. However, mercury continues to be present in sediments of the northwest corner of Squamish Harbour. After 10 yr, crabs and bottom fishes of the upper end of Howe Sound, although less contaminated than in 1970, continue to exhibit mercury concentrations that are higher than background, and in some cases exceeding the upper limit of 0.5 μg·g wet wt^{-1} set by the Food and Drug Directorate for commercial utilization of fish products.

Petroleum refineries — There are four petroleum refineries that could contribute to pollution reaching the Strait of Georgia. These are all concentrated at the upper end of Burrard Inlet, including Port Moody. They are modest sized refineries, each processing from 30 000 to 50 000 bbl (4000−7000 t) of crude oil per day. Effluents from the refineries may contain assorted plant wastes, including traces of oil. At one time, Port Moody was occasionally heavily covered by an oil film. But this is now the rare exception, rather than the rule, because the refineries have "generally tightened up on losses" of valuable crude oil and refinery products. Surveys of oil pollution in Burrard Inlet have shown concentrations everywhere, including Port Moody, to be less than 1 μg·L^{-1} (ppb), using the fluorescence method based on chrysene as a standard. The values could be higher by a factor of 10 if the fluorescence measured were compared with a whole oil standard (D. R. Green, Seakem Oceanography Ltd., Sidney, B.C., personal communication).

The main water pollution that could now arise from operation of the petroleum refineries is through entry of oil into the sea due to accidental spillage during transfer from tanker to refinery or undetected leakage of crude oil or refinery products from the plant, tanks, or piping.

Other chemical plants — There are few other chemical plants in British Columbia that contribute significant amounts of waste into the Strait of Georgia. Assorted small operations on the lower Fraser River, among which the Dow Chemical Canada Inc. plant producing phenolic resins is the most noteworthy, discharge effluents into the river. Effluent containing phenols is produced by the Dow plant, but it is held in a biological treatment pond to reduce the phenolic content before discharge. A chemical plant of Reichhold Ltd. in Barnet occasionally releases some effluents into Port Moody that may sometimes cause turbidity and discoloration of the water because of the precipitation of hydroxides.

Agricultural runoff — There is rather limited agriculture bordering on the Strait of Georgia. Much of the agricultural runoff of the Fraser Valley is received by the lower Fraser River, where it may undergo various transformations in the river and estuary before reaching the Strait of Georgia. The other main inputs of agricultural runoff are in Boundary Bay through the Serpentine and Nicomekl rivers and into Baynes Sound through the Courtenay River and other smaller streams draining the Comox Valley. There is minor agricultural runoff from small farms along the east coast of Vancouver Island.

Drainage from farms may contain residues from fertilizers and pesticides used in normal agricultural practice. Nutrients and bacteria can be contributed by excreta of farm animals. Nutrients derived from farm drainage may have been partly responsible for the blooms of dinoflagellates that led to paralytic shellfish poison accumulated by clams and oysters in Baynes Sound during 1957 (Waldichuk 1958b). Coliforms from farm animals could have contributed to the closure of shellfish beds in Boundary Bay.

The impact of agricultural runoff on the water quality in the Strait of Georgia is probably comparatively small, but, as a non-point source, the effects of such runoff are difficult to quantify and control.

Forest-related sources — Various forestry activities can contribute to environmental degradation in the Strait of Georgia. Poor logging practices may lead to severe erosion, and even landslides, in watersheds. Runoff carries with it both organic and inorganic particulate material that leads to siltation in the streams and estuaries. Perhaps the most adverse effect occurs on spawning grounds in streams. However, the ecological conditions in estuaries may also be unfavorably altered by deposition of material eroded from logged-over areas. Perhaps the major effect of logging, in this sense, on the waters of the Strait of Georgia and the living resources that they nurture stems from logging activities in the Fraser River drainage basin. Other streams draining into the Strait of Georgia may suffer from the same kind of impact but on a much smaller scale. Happily, improved logging practices are reducing such environmental degradation.

The other source of environmental problems associated with forest harvesting is in log-booming activities. While the trend is to dry-land sorting and reduced inventories of logs at tidewater, there are still numerous log-holding sites around the periphery of the Strait of Georgia. In addition to the benthic deterioration that can take place, leachates from wood and bark can impair water quality. There is undoubtedly a gradation of effects, which vary from those associated with infrequent use of a log-holding area to those arising from intensive turnover of inventory in a log pond. The latter may cause heavy deposition of wood chips and bark, which is not a favorable environment for invertebrates and fish. Unfortunately, the effects of log-booming activities on marine life have not yet been fully evaluated, and the point at which damage becomes severe and acutely detrimental to the living resources is not known.

Concentrations of Critical Pollutants

The substances that are considered "critical pollutants" are those which are persistent, may be bioaccumulated, and may also be toxic. They could lead to an accumulation in the Strait of Georgia if the input exceeds the output. Biodegradable substances are usually not in this category. Also, such nonconservative substances as the plant nutrients are not considered to be critical pollutants. This is not to say that these

substances do not cause local problems, or if present in large enough volume, do not create a large-scale problem. The critical pollutants normally considered are petroleum hydrocarbons, organohalogens, metals, persistent solids, and radionuclides. Since we have no nuclear reactors or other potential radioactive sources on the Pacific coast of Canada, except for incidental wastes from radioisotope tracer work in hospitals and chemical, biological, and other laboratories and the remaining worldwide fallout from nuclear weapons testing, we can eliminate radionuclides from the outset. As we proceed with our review of the other groups of substances, it will become rapidly evident that we are sadly lacking in our knowledge of the concentrations of these substances in the water, sediments, and biota of the Strait of Georgia.

Petroleum Hydrocarbons

The Strait of Georgia can be considered from the point of view of oil pollution as a typical semienclosed coastal sea with a modest population along its shores, most of it being concentrated on the southeast side, and a moderate amount of sea traffic, some of it conveying crude oil and refined products across the Strait to and from refineries. In that sense, it can be expected that, in the absence of a major oil spill, the amount of oil in its waters, sediments, and biota would be quite small. This appears to be the case from the very limited information that we have on hand. The bunker fuel oil spill of about 200 t from the freighter *Erawan* in September 1973 that resulted from a collision with the container ship *Sun Diamond*, at the entrance to Burrard Inlet, was the largest oil spill we have had in the last decade. From time to time, there are incidental spills of fuel oil or other petroleum products, amounting to a few hundred litres, but these are not substantial as contributions to petroleum hydrocarbons in the whole Strait of Georgia. It has been estimated that there is an annual total oil spillage from all Canadian sources into the Strait of Georgia–Juan de Fuca Strait system of about 22 000 bbl (3000 t) compared with about 41 000 bbl (5600 t) from United States sources (Oceanographic Institute of Washington 1980). The sources of oil input included tankers in transit and at berth, storage tanks, pipelines, tank barges, non-oil-transporting vessels, and land sources consisting of coastal refineries, municipal wastewater, urban runoff, and marine and land transportation facilities. It is noteworthy that the acute sources of oil spillage risk amounted to about 2000 bbl (272 t) from the Canadian side and 4000 bbl (544 t) from the American side annually, or about 10% of the total inputs.

The focus of the oil industry along the Strait of Georgia is in the east end of Burrard Inlet, where four refineries and a gas-fired, thermal electricity generating plant are located. Studies have been conducted by federal government agencies in this area (Waldichuk 1965b; Waldichuk et al. 1968) and by consultants (T. W. Beak Consultants Ltd. 1969) to note the effect of the petroleum refineries and other waste sources on the environmental and biological characteristics of this body of water. Depressed dissolved oxygen levels in Port Moody during late summer were particularly evident, but this condition did not appear to limit the success of the most prevalent animal groups. The environmental conditions in Port Moody have improved in the last 10 yr because of better control of municipal wastewater and refinery discharges. Oil slicks are no longer as common now as they were in the 1950s and 1960s.

Recent studies of oil pollution in Burrard Inlet (D. R. Green, Seakem Oceanography Ltd., Sidney, B.C., unpublished data) provided data on oil concentrations at a series of stations that could be compared with those of the more polluted waters of False Creek and near the Iona Sewage outfall, as well as the cleaner waters at Sand Heads, Active Pass, and in Saanich Inlet. Values for total oil by the fluorescence technique, and chrysene as a standard, ranged from 0.77 $\mu g \cdot L^{-1}$ for waters receiving oil refinery effluents in Port Moody to 0.13 $\mu g \cdot L^{-1}$ in Active Pass.

Sampling for particulate oil residues (tar balls) in the Strait of Georgia during the early 1970s gave largely negative results (Green 1976). During 28–30 November 1972, 36 neuston tows were made between Active Pass and Texada Island. No particulate oil residues were found in 34 of these tows. In the remaining two tows, there were indications of oil, but these were difficult to quantify. Beach surveys between Victoria and Saanich Inlet during June and July of 1973 failed to show the presence of any tar balls (W. Cretney, Institute of Ocean Sciences, Sidney, B.C., personal communication).

Summed concentrations of 10 aromatic hydrocarbons along the southeastern shore of the Strait of Georgia, on the American side of the border, ranged approximately from 5 to 20 $\mu g \cdot kg$ dry wt^{-1} in the intertidal sediments and from 40 to 175 $\mu g \cdot kg$ dry wt^{-1} in mussels, *Mytilus edulis* (Kopenski and Long 1981). Attempts to relate the presence of polycyclic aromatic hydrocarbons to tumors in shellfish and finfish have led to analyses of benzo[*a*]pyrene in mussels (*M. edulis*) and nearshore sediments of the southern Strait of Georgia and contiguous waters (Dunn and Stich 1976; Stich et al. 1977). The concentration of benzo[*a*]pyrene in mussels exhibited a seasonal variation, with maximum concentrations in winter of more than 30 $\mu g \cdot kg$ wet wt^{-1} for mussels from False Creek, which decreased to 10 $\mu g \cdot kg$ wet wt^{-1} in the summer. The corresponding seasonal variation in outer English Bay was from 9 to 2 $\mu g \cdot kg$ wet wt^{-1} (Dunn and Stich 1976). Concentrations in sediments ranged from 0.1 $\mu g \cdot kg$ wet wt^{-1} at the southern end of Baynes Sound to 80 $\mu g \cdot kg$ wet wt^{-1} in Budd Inlet near Olympia, WA (Fig. 10). No relationship could be found between the concentration of benzo[*a*]pyrene and the incidence of tumors in English sole, *Parophrys vetulus*.

In the continuing absence of major oil spills in the Strait of Georgia or in its contiguous waters, the amount of oil in the water, sediments, and biota will probably remain small. However, increased transportation of oil through Juan de Fuca Strait into Puget Sound and to refineries in Washington State near the 49th parallel could pose a higher risk of oil pollution in the Strait of Georgia. Not only could the shores become polluted from surface oil slicks, but a greater hazard could arise from oil pollution in the deep water because of vertical mixing and subsurface penetration at the southern entrance to the Strait. While the likelihood of exploitation for oil in the Strait of Georgia remains small, the recent report of the Geological Survey of Canada identifies a geological zone known as the Nanaimo Basin, with potential for oil and gas, which essentially lies beneath the waters of the Strait of

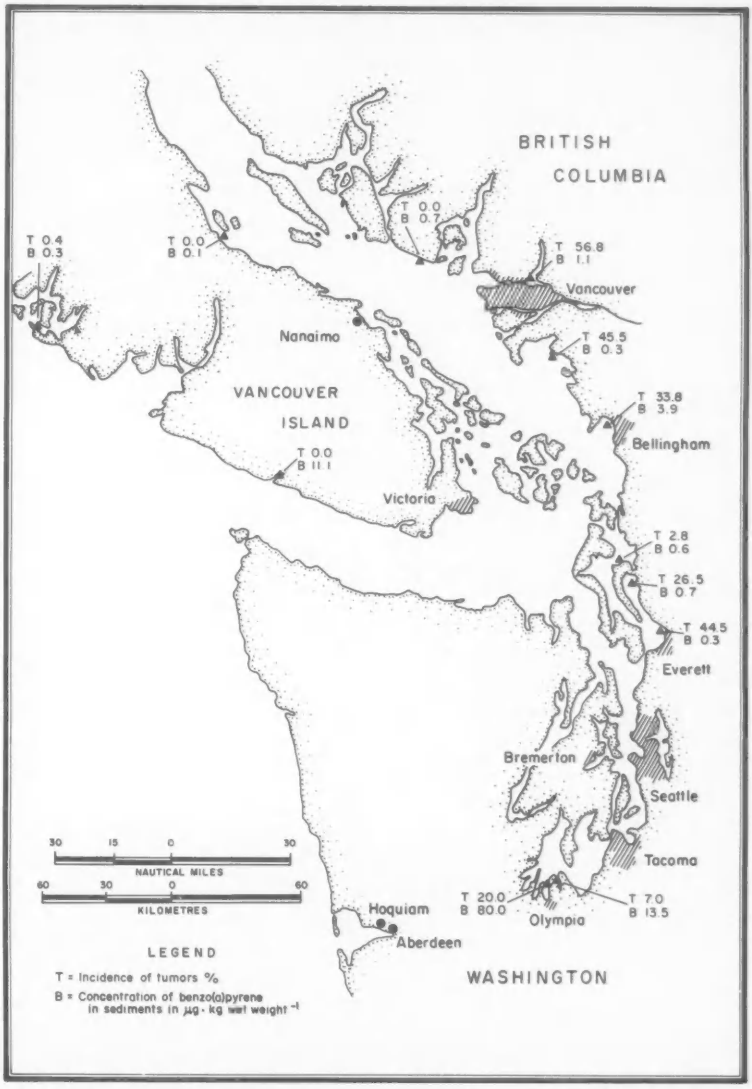

FIG. 10. Distribution of benzo[*a*]pyrene (*B*, micrograms per kilogram wet weight) in sediments of the southern Strait of Georgia and Puget Sound and incidence of tumors (*T*, percentage) in English soles (*P. vetulus*). (From Stich et al. 1977)

Georgia between Quadra Island in the north and the Gulf Islands in the south (Haimila and Proctor 1982; Yorath and Cameron 1982). A small strip of this zone runs along the east coast of Vancouver Island between Ladysmith and Campbell River, and already the provincial government has opened 5212 ha in the Oyster Land District for oil and gas exploration and has called for competitive bids from the oil industry.

ORGANOHALOGENS

These compounds are of particular concern, because they are generally long-lived in the environment, are often toxic, and can be bioaccumulated by aquatic organisms. The common representatives of this group of chemicals are the pesticide DDT and the industrial chemicals polychlorinated

biphenyls (PCBs). DDT was never extensively used in British Columbia either in forestry to control defoliators or in agriculture. It was used to some extent in the interior of the province to control mosquitos and could have entered the drainage basin of the Fraser River from that source. However, DDT and its metabolic products are not expected to be present in significant concentrations in the Strait of Georgia. PCBs have been used in electrical transformers and condensers throughout British Columbia. While there have been some leaks and spillages of PCBs, none has been reported of any size that would significantly affect the waters and biota of the Strait of Georgia.

No organochlorines have been detected in waters or sediments of the lower Fraser River, its estuary, or in the Strait of Georgia in analyses conducted during the early 1970s (Hall et al. 1974; Oloffs et al. 1972; Oloffs et al. 1973). More advanced techniques of analysis available today would undoubtedly detect organochlorines in all media of the Strait of Georgia, even though they may be present in very small concentrations. A study of chlorinated hydrocarbons in biota of the Fraser River Estuary and the Strait of Georgia during 1972–73 (Albright et al. 1975) showed the presence of dieldrin, *p,p'*-DDT, *p,p'*-DDD, *p,p'*-DDE, heptachlor epoxide, and PCBs in many fishes and benthic organisms of the lower Fraser River and its estuary. Mean values of *p,p'*-DDT, *p,p'*-DDE and PCBs reported for Fraser River fish in that investigation were 0.3, 40.5, and 140.8 $\mu g \cdot kg^{-1}$, respectively. These values were lower by at least an order of magnitude compared with the concentrations of the same compounds in fish from 50 sampling locations across the United States. Except for low mean levels of *p,p'*-DDE (mean of 2.1 $\mu g \cdot kg^{-1}$) in three of seven samples of Dungeness crab, *Cancer magister*, taken from Cowichan Bay, no chlorinated hydrocarbons were found in fish or crabs captured in the Strait of Georgia away from the immediate influence of Fraser River water (Albright et al. 1975).

Metals

By their physical and chemical nature, metals are persistent, but they can be transformed into different physical states and chemical forms. They are toxic and can be bioaccumulated to high concentrations by aquatic organisms. While some metals, e.g. copper, zinc, magnesium, and cobalt, are required in low concentrations for proper nutrition in plants and animals, other metals, such as mercury, cadmium and lead, have no known nutritive role. The latter metals are also highly toxic, mercury having become infamous through Minamata disease, cadmium causing *Itai itai* affliction, and lead producting neurological, blood, and kidney damage in humans.

Analytical data for metals in water have always suffered from problems of contamination during sampling and analysis, as well as from inadequate methodology in terms of sensitivity and precision. As a result, early data almost always gave too-high metal concentrations, and if one examines year-to-year trends in metal levels, one is liable to be deceived into concluding that there is a decline. For this reason, unless there is a way of correcting early metal data to be comparable with present-day data, the early data on metal concentrations have value only for relative purposes, such as distributions of metals vertically or horizontally in a body of water at the time. The Strait of Georgia is no exception in this regard, and data on metal concentrations in seawater must be examined very critically when these are compared from year to year. This particularly applies to lead-in-seawater analysis, which is difficult to perform, and it has been stated by the expert on lead analysis, Dr C. C. Patterson at the California Institute of Technology, Pasadena, CA, that if the concentration of lead measured in deep Pacific Ocean seawater exceeds 1 $ng \cdot L^{-1}$, there has undoubtedly been contamination in sampling and/or analysis (Schaule and Patterson 1980).

Several studies of metals in the Strait of Georgia and contiguous waters have been conducted by graduate students at the Department of Oceanography (formerly Institute of Oceanography), University of British Columbia, under the supervision of Dr E. V. Grill. These included an investigation of copper and lead in waters of Burrard Inlet and Indian Arm (Erickson 1973), a study of the effects of the sediment-exchange reactions in the Fraser River Estuary on zinc and copper distributions in the Strait of Georgia (Thomas 1975; Thomas and Grill 1977), and the chemistry of manganese in the Fraser River Estuary as well as the distribution of this element in the estuary and the Strait of Georgia (de Mora 1981). Lead is one metal that distinctly shows the effects of man-made input through runoff and precipitation, with highest levels exhibited at the sea surface.

It was clear at least in the last two studies that the Fraser River plays a vital role in the distributions of such metals as zinc, copper, and manganese in the Strait of Georgia. Both copper and zinc concentrations in seawater increased during spring and early summer when the Fraser River discharge and the river sediment load were highest (Fig. 11). These increases could not be attributed to the dissolved metals in the river water but were apparently caused by the desorptive processes occurring when the river sediment mixed with seawater (Thomas and Grill 1977). On the other hand, manganese is released from sediments, and possibly interstitial water, into seawater when the Fraser River Estuary sediments are resuspended during high river flows (de Mora 1981). Entrainment of seawater from the toe of the salt wedge in the river into the outflowing river water causes a downstream increase in manganese. In the Strait of Georgia, manganese exhibits a maximum at salinities ranging from 4 to 12‰ and decreases with increasing distance from the Fraser River Estuary. Both dissolved and particulate manganese profiles at a station in the middle of the Strait of Georgia exhibited concentrations of about 1 $\mu g \cdot L^{-1}$ at the surface and 10–12 $\mu g \cdot L^{-1}$ at a depth of 400 m. The high near-bottom concentrations were believed to be due to oxidative precipitation of manganese and/or the resuspension of bottom sediments (de Mora 1981).

Most of the other studies of metals in seawater of the Strait of Georgia and contiguous waters have been conducted by Dr C. S. Wong and colleagues at the Institute of Ocean Sciences, Patricia Bay. If Saanich Inlet waters can be considered comparable with those of the Strait of Georgia, then the following total metal concentrations (nanograms per litre) can be considered as representative: Hg, 5; Cu, 500–600; Ni, 300–350; Zn, 600; Cd, 70–80; Co, 26; Fe, 300–400;

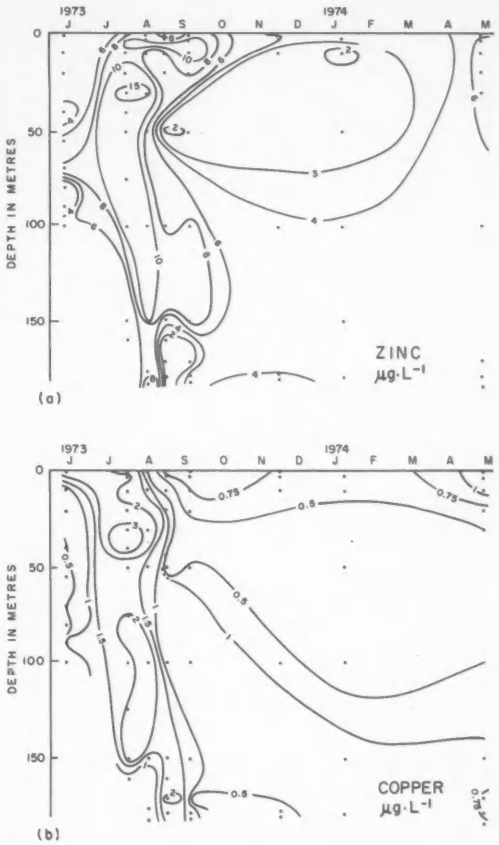

FIG. 11. Seasonal variations of concentrations (micrograms per litre) of (a) dissolved zinc and (b) copper at a station in the Strait of Georgia about 14 km off the main arm of the Fraser River. (From Thomas and Grill 1977)

Mn, 300–400 (Wong et al. 1977). Lead values (nanograms per kilogram) for surface seawater have been reported (Stukas and Wong 1981) as follows: English Bay in Burrard Inlet, total 170 ± 2, dissolved, 100 ± 2; Haro Strait, total 30 ± 2; Saanich Inlet, total 24 ± 2; Patricia Bay, total 36.6 ± 0.4; Juan de Fuca Strait, near Victoria, total 19 ± 1. These values have been checked with good agreement by analysis of some samples at the laboratory of Dr C. C. Patterson (Stukas and Wong 1981).

Further information for metals in the Strait of Georgia and tributary waters is given for the Fraser River water and fish and for sediments and biota in the estuary in various publications and reports (Parsons et al. 1973; Benedict et al. 1973; Hall et al. 1974; Northcote et al. 1975; P. M. Chapman et al., E. V. S. Consultants Ltd., North Vancouver, B.C., unpublished data; Grieve and Fletcher 1976; Fletcher et al. 1983). In many cases, elevated levels of metals, especially mercury, mercury, were found in fish of the river and in crabs and sediments in the estuary near the Iona Island sewage outfall. Studies have also been conducted on the Point Grey dumpsite, particularly with respect to release of metals by dredge spoils and uptake by marine organisms (Hoos 1977a, 1977b; Packman 1980; Thompson and Paton 1978, 1980; C. S. Wong et al., Institute of Ocean Sciences, Sidney, B.C., unpublished data). There has been no conclusive evidence for leaching of metals from the dredge spoils and uptake by the cucumber *Molpadia intermedia*. In fact, there appeared to be a decline in copper, zinc, and cadmium in the sea cucumber from 1976 to 1977 (Thompson and Paton 1980). The authors suggested that *M. intermedia* is not a suitable organism for monitoring purposes because of its wide natural variability in metal content.

Concentrations of various metals (e.g. copper, zinc, and lead) have been determined in the common blue mussel, *M. edulis*, taken at a number of points in the southern Strait of Georgia, Howe Sound, and Burrard Inlet (Stump et al. 1979; Popham et al. 1980). Mussels taken from the vicinity of storm drains exhibited much higher levels of metals, especially lead, than those only 30 m away from the point source.

Copper and zinc have been measured in sediments of the Strait of Georgia in the vicinity of the Texada mine (Thompson et al. 1979), which ceased operating in 1976. Copper concentrations of up to 1600 $\mu g \cdot g$ dry wt^{-1} at stations within 1.8 km of the outfall were reported. But these concentrations rapidly decreased with distance from the outfall, background levels (<50 $\mu g \cdot g$ dry wt^{-1}) being reached at about 10 km. Zinc levels ranged from 30 to 200 $\mu g \cdot g$ dry wt^{-1} but showed no clear trend with distance from the mine. Sedimentary levels of metals have also been measured in the area of Cape Lazo, near Comox (Clague 1976). Concentrations of lead in the sediments appeared to be considerably above background, and the author was unable to account for these.

One can conclude from the available information that the waters of the Strait of Georgia as a whole exhibit metal levels that are typical of coastal waters that have not been excessively polluted. There are mild "hot spots," such as the Fraser and Squamish estuaries, where metals are found above background levels in the sediments and marine organisms. Certain long-lived species of fish, such as spiny dogfish, *Squalus acanthias*, may exhibit levels of mercury in the older specimens above the permissible limit of 0.5 $\mu g \cdot g$ wet wt^{-1} established for commercial use; the origin of this mercury appears not to be necessarily anthropogenic, but likely natural sources in seawater and food eaten by dogfish. Shellfish are vulnerable to bioaccumulation of metals, and in areas where mine effluents or tailings are present, e.g. Howe Sound and Texada Island, oysters and mussels may exhibit extremely high concentrations of copper and zinc.

PERSISTENT SOLIDS

This group of substances may include both inorganic and organic materials. Mine tailings are a good example of inorganic materials, and persistent plastics are representative of organic solids. In the Strait of Georgia there is no active mining operation with tailings disposal into the sea, although

tailings remain in the waters adjacent to the former mines at Britannia in Howe Sound and at Texada Island in the Strait of Georgia. Dredge spoils are the material belonging to this category that is dumped at present in largest volume into the Strait of Georgia (Hoos 1977a). Provided there are no noxious substances in these dredge spoils, their main impact is a physical one, whereby benthic organisms and habitats are obliterated. With some exceptions, recolonization of dumpsites can be relatively rapid once dumping operations have ceased. Designated dumpsites at selected locations reduce to a minimum the area of impact by dumping dredge spoils in that they avoid proliferation of new dumping sites.

The Strait of Georgia receives its share of garbage and litter from vessels as well as from onshore activities. This is now being controlled by the Canadian Coast Guard at least for larger vessels under the Canada Shipping Act and, to some extent, by self-discipline on board commercial fishing vessels and recreational boats. Refuse from shore is also being controlled in various ways through antilitter campaigns.

The big problem of solids in the Strait of Georgia, however, stems from flotsam and jetsam that is washed down by rivers, particularly the Fraser when it is in freshet. Logs and uprooted trees, along with other debris, may be introduced into the Strait of Georgia during the large flow of the Fraser River in May and June. This creates a serious problem for smaller boats and even for larger vessels, which may sustain damage during collisions with this floating material. Not only does this amount to more than $1 million per year in vessel damage but also poses a risk to human safety. Whereas in countries that are short of wood, these floating sources of energy and building material would be eagerly picked up, costly cleanup programs must be instituted to remove this material from coastal waters of British Columbia. In 1977, it was estimated that 0.24 M (million)$\cdot m^{-3}$ (8.6 M$\cdot ft^{-3}$) of waterborne debris, including logs and other wooden refuse, were recovered from British Columbia waterways, most of it from the Fraser River and the Strait of Georgia (Waldichuk 1978). The British Columbia Ministry of Forests carried out in 1971 an extensive study of debris in a number of rivers and boating areas and came to the conclusion that such material could be classified into three categories: natural, 37%; man-made waste, 32%; and sawlogs, 31%. With the increasing energy needs, there is obviously a resource here that should be tapped rather than leaving it as a liability.

The available data on "critical pollutants" in water, sediments, and tissues of marine organisms in the Strait of Georgia are summarized in Table 1. Data are rather fragmentary and come from a variety of sources. The reader is cautioned to examine the original data before using this information for any evaluative or waste management purposes.

Impact of Pollution on Living Resources

It is difficult to establish a clear-cut effect of pollution on fisheries in the Strait of Georgia. There are so many other factors that must be considered, such as fishing effort and natural variability, which could have a significant effect on fish stocks. In other words, the signal-to-noise ratio is small. While there may be fish kills in areas adjacent to pulp mills, chloralkali plants, or sewage outfalls, the effect of such kills on a whole population may be insignificant.

Shellfish

Perhaps the one effect of pollution on a living resource that can be clearly documented in the Strait of Georgia is the effect of sewage on molluscan shellfish. Oysters, clams, and mussels are filter feeders, and they can concentrate bacteria and viruses present in the water along with phytoplankton. Such human afflictions as hepatitis and gastroenteritis can be transmitted through the consumption of raw or only partially cooked shellfish. The coliform count can exceed acceptable levels for shellfish harvesting in areas exposed to sewage effluent that has not been disinfected. Closure is enforced in shellfish areas that cannot meet the established bacterial standards for shellfish waters and shellfish meat under federal regulations. Pacific oyster (*Crassostrea gigas*) culture has been particularly hard hit in the Strait of Georgia, with oyster harvesting banned in some areas and restricted (oysters must undergo depuration before marketing) in others. About one-fifth of existing oyster leases have been closed for oyster harvesting. A large proportion of potential oyster growing areas has been closed in the past. Noteworthy among these are leases in Boundary Bay, Baynes Sound, Ladysmith Harbour, Pender Harbour, Stuart Channel, and Desolation Sound. Clam digging is banned in many other areas near urban communities, e.g. Nanaimo and Vancouver harbours. The problem does not appear to diminish. About 54 400 ha of intertidal and subtidal areas in British Columbia are closed to the taking of shellfish because of fecal contamination. Most of the closures are in the Strait of Georgia, where 49 200 ha, involving 82 closures, are banned for shellfish harvesting. Of these, the largest closure covers 38 600 ha, or approximately 78% of the total closure area, and comprises Boundary Bay, the Fraser River Estuary, and Vancouver Harbour. Urban and agricultural runoff contributes to the problem. At the time of writing (February 1982), there were 219 foreshore leases comprising 898 ha of oyster-growing area in the Strait of Georgia. About 152 ha, or 17% of the oyster-growing area in the Strait, were closed owing to excessive fecal coliform count (B. Kay, Environmental Protection Service, West Vancouver, B.C., unpublished data).

Shellfish are also affected by other pollutants, such as metals, which they bioaccumulate (Waldichuk 1974; Ellis et al. 1981). Oysters that have high concentrations of copper turn green and tend to have a metallic flavor. If they exceed the limiting concentrations of metals established for human consumption by the Food and Drug Directorate, they are banned from the market.

Pollution may affect the condition and survival of shellfish. This has not been too well documented in the Strait of Georgia. Oysters (*C. gigas*) in the vicinity of the pulp mill at Crofton declined in condition factor and flavor after the mill went into operation in 1958 (Quayle 1964; Ellis et al. 1981). The cause of this decline in quality of the oysters in Stuart Channel has not been clearly established, but it is undoubtedly related to some unfavorable effects of the pulpmill effluent.

An indirect effect on molluscan shellfish from excessive enrichment of waters by nutrients from sewage and agricultural runoff may be blooms of toxic dinoflagellates, e.g. *Gonyaulax* sp., which are concentrated by clams, mussels, and oysters and cause paralytic shellfish poisoning in

TABLE 1. Summary of concentrations of "critical pollutants" in different media of the Strait of Georgia. Concentration units are as follows, unless otherwise indicated. Water: $ng \cdot L^{-1}$; sediments: $mg \cdot kg$ dry wt^{-1}; tissue (*M. edulis*): $\mu g \cdot kg$ wet wt^{-1} (petroleum hydrocarbons and organohalogens), $mg \cdot kg$ dry wt^{-1} (metals); $n \cdot L^{-1}$ = ppt, $mg \cdot kg^{-1}$ = ppm, $\mu g \cdot L^{-1}$ = ppb, $\mu g \cdot kg^{-1}$ = ppb.

	Water	Sediments	Tissue
Petroleum hydrocarbons	0.13–0.77[a] $\mu g \cdot L^{-1}$	5–20[g] 0.1–3.9[h] $mg \cdot kg$ wet wt^{-1}	470–175[g] $\mu g \cdot kg$ dry wt^{-1} 2–10[h]
Organohalogens			
p,p'-DDT			0.3[m]
p,p'-DDE			40.5[m] (23.0–296)[n] 2.1[o]
PCB		0.39 (0.08–1.40)[i]	140.8[m] 782 (234–2100)[n] 559 (170–1375)[p] 2724[q] 295[r] 193[s] 0.54 (0.160–1.72)[t] 0.26 (0.157–0.492)[u] 0.021 (0.009–0.031)[v]
Metals			
Hg	5[b]	0.53 (0.18–1.23)[j] 0.39 (0.27–0.51)[k]	1.74 (0.37–3.7)[w] 0.36 (0.18–0.90)[x] 0.22 (0.15–0.44)[y]
Cd	70–80[b]	<2.0[j] 0.27 (<0.2–0.5)[k]	1.7±1.4 (0.5–6.7)[z] 1.4±1.3 (0.1–5.4)
Pb	30–170[c] 330 (310–380)[d] (1–3 m) 90 (80–100)[d] (220–225 m)	12.5 (6.1–43.0)[j] 23 (17–31)[k] 18.2 (11.2–27.7)[l] (0–5 cm) 12.9 (7.4–17.9)[l] (50–55 cm) 10.4 (4.3–15.0)[l] (68–73 cm)	1.4±0.7 (0.4–3.7)[z]
Cu	500–3000[c]	37.7 (26.1–47.1)[j] 48 (41–57)[k] 45.9 (38.3–59.5)[l] (0–5 cm) 43.2 (37.8–49.9)[l] 50–55 cm) 41.9 (37.6–50.3)[l] (68–73 cm)	26±14 (6–63)[z]
Zn	600[b] 2000–15 000[c]	91.4 (67.5–128.6)[j] 101 (76–124)[k] 102.3 (87.5–113.1)[l] (0–5 cm) 95.6 (87.3–105.0)[l] (50–55 cm) 90.6 (84.5–104.1)[l] (68–73 cm)	171±55 (108–375)[z] 139±12 (118–167)
Co	26[b]	14.2 (10.7–16.9)[j] 13.5 (10.4–16.1)[l] (0–5 cm) 13.6 (10.2–15.8)[l] (50–55 cm) 13.8 (10.6–16.4)[l] (68–73 cm)	
Ni	300–350[b]	39.7 (27.9–46.3)[j] 48.6 (41.3–53.9)[l] (0–5 cm) 48.2 (39.1–54.7)[l] (50–55 cm) 49.2 (40.1–61.9)[l] (68–73 cm)	
Mn	300–400[b] 100–1400[f]	337.5 (286.0–452.2)[j] 330.3 (291.2–373.8)[l] (0–5 cm) 319.0 (283.7–366.7)[l] (50–55 cm) 326.4 (286.1–369.4)[l] (68–73 cm)	
Fe	300–400[b]	2.78 (2.06–3.17)%[j] 3.4 (2.8–3.8)%[l] (0–5 cm) 3.5 (2.8–4.0)%[l] (50–55 cm) 3.5 (2.7–3.8)%[l] (68–73 cm)	
Cr			2.2±1.8 (0.4–7.9)[z]

[a]Total oil concentration by the fluorescence analytical technique and chrysene as a standard. Values could be greater by a factor of 10 if whole oil standards were used (D. R. Green, Seakem Oceanography Ltd., Sidney, B.C., unpublished data and personal communication).

TABLE 1. (*Continued.*)

[b]Values represent analyses of water from Saanich Inlet (Wong et al. 1977).

[c]Data from Stukas and Wong (1981).

[d]Mean (range in parentheses) of dissolved Pb concentrations at a station in the Strait of Georgia near the entrance to Burrard Inlet at 1–3 and 200–225 m (Erickson 1973).

[e]Seasonal range in dissolved Cu and Zn concentrations in the water column from the surface to 175 m at a station in the Strait of Georgia about 14 km west of the main arm of the Fraser River (Thomas and Grill 1977).

[f]Seasonal range of dissolved Mn at and near the surface in the Strait of Georgia, between the Fraser River Estuary and Vancouver Island (de Mora 1981).

[g]Summed concentrations of 10 aromatic hydrocarbons in sediments and mussels, *M. edulis*, on the southeast shores of the Strait of Georgia (Kopenski and Long 1981).

[h]Benzo[*a*]pyrene concentrations in sediments and mussels, *M. edulis*, at a few shore stations in the Strait of Georgia (Dunn and Stich 1976; Stich et al. 1977).

[i]Mean (range) of PCB concentrations for sediment samples collected in False Creek, January 1982 (Willis Cunliffe Tait/DeLCan 1982). Dredge spoils from False Creek are normally dumped at the Point Grey dumpsite, 49°15.4′N, 123°22.1′W.

[j]Mean (range) of metal concentrations for 30-cm cores taken in and around the Point Grey dumpsite during 1978 (Packman 1980).

[k]Mean (range) of metal concentrations for cores to 70-cm depth taken in March 1982 at the Point Grey dumpsite (D. E. Brothers, Environmental Protection Service, West Vancouver, B.C., unpublished data).

[l]Mean (range) of metal concentrations for different segments of cores taken in and around the Point Grey dumpsite during 1975 at depths of 0–5, 50–55, and 68–73 cm (Hoos 1977b).

[m]Mean values of DDT, DDE, and PCB concentrations in Fraser River fish (Albright et al. 1975).

[n]Range of DDE concentrations and mean (range) of PCB concentrations in crabs, *C. magister*, taken on Sturgeon Bank in the Fraser River Estuary (Albright et al. 1975).

[o]Mean value of DDE concentration for three of seven samples of crab, *C. magister*, taken in Cowichan Bay (Albright et al. 1975).

[p]Mean (range) of PCB concentrations in crabs, *C. magister*, taken on Roberts Bank in the Fraser River Estuary (Albright et al. 1975).

[q]Mean PCB concentration in Pacific oysters, *C. gigas*, from Roberts Bank in the Fraser River Estuary (Albright et al. 1975).

[r]Mean PCB concentration in ghost shrimp, *Callianassa californiensis*, from Sturgeon Bank in the Fraser River Estuary (Albright et al. 1975).

[s]Mean PCB concentration in the clam, *Cardium corbis*, from Roberts Bank in the Fraser River Estuary (Albright et al. 1975).

[t]Mean (range) PCB concentration in spiny dogfish, *S. acanthias*, from coastal waters of British Columbia (Department of Fisheries and Oceans, Fish Inspection Laboratory, Vancouver, B.C., unpublished data).

[u]Mean (range) PCB concentration in Pacific herring, *C. harengus pallasi*, from coastal waters of British Columbia (Department of Fisheries and Oceans, Fish Inspection Laboratory, Vancouver, B.C., unpublished data).

[v]Mean (range) PCB concentration in sockeye salmon, *O. nerka*, from coastal waters of British Columbia (Department of Fisheries and Oceans, Fish Inspection Laboratory, Vancouver, B.C., unpublished data).

[w]Mean (range) of Hg concentrations in crabs, *C. magister*, taken on Sturgeon Bank of the Fraser River Delta, which received effluent from the Iona Island Sewage Treatment Plant (Parsons et al. 1973).

[x]Mean (range) of Hg concentrations in crabs, *C. magister* and *C. productus*, from Roberts Bank of the Fraser River Delta (Parsons et al. 1973).

[y]Mean (range) of Hg concentrations in crabs, *C. magister* and *C. productus*, taken from Cowichan Bay, 48°45′N, 123°37′W (Parsons et al. 1973).

[z]Mean ± standard deviation (range) of metal concentrations in sea cucumbers, *M. intermedia*, taken during March 1976, at the Point Grey dumpsite (Thompson and Paton 1978). The values directly below (for Cd and Zn) represent mean ± standard deviation (range) of metal concentrations in *M. intermedia* taken during July 1977 at the Point Grey dumpsite (Thompson and Paton 1980).

consumers, as occurred in Baynes Sound in 1957 (Waldichuk 1958b).

SALMONIDS

Although salmonids and their habitats can be affected by pollution, any adverse effects are not as easily demonstrated as with oysters. Pulpmill effluents are known to be toxic and lead to oxygen deficiency in the receiving waters, but there have been no recorded incidents of salmonids being acutely affected by such conditions in the Strait of Georgia. The most serious problems could be expected to occur in the estuaries, where juvenile salmonids feed for various periods before they proceed to sea. The Fraser River Estuary, of course, could pose serious problems in this regard if pollution were allowed to become severe. The adverse effects on fish of low dissolved oxygen in the water adjacent to the Iona Island Sewage Treatment Plant have been recorded (I. K. Birtwell, West Vancouver Laboratory, West Vancouver, B.C., unpublished data), but the in situ observations of distressed fish involved flatfish species, predominantly starry flounders, *Platichthys stellatus*.

HERRING

Pacific herring, *Clupea harengus pallasi*, are most vulnerable to the harmful effects of pollution during their egg and larval stages. An oil spill near a herring spawn could wipe out

the progeny before they hatch in the affected area because of the propensity of the Pacific species to spawn in the intertidal or shallow subtidal zones and the tendency of oil to drift ashore. Herring spawning substrate could be unfavorably affected for a long time by oil and other clinging pollutants. Undoubtedly, this has already occurred in spawning habitats along some shorelines but has not been documented.

Herring larvae spend some time in the upper layer of the sea before they metamorphose into juveniles. They are highly sensitive to almost any pollutant at this time. Larvae would be particularly vulnerable to toxic substances introduced at the sea surface either through river discharge or by shallow outfalls. No such incidents have been recorded, however, in the Strait of Georgia so far.

Groundfish

Species of groundfish, such as Pacific cod, *Gadus macrocephalus*, which spawn on the sea bottom, can have their spawning grounds destroyed by ocean dumping of dredge spoils or other solid materials. Other species, such as English sole, *Parophrys vetulus*, whose eggs are pelagic, could conceivably be affected by sea surface pollutants, including oil. None of these adverse effects has yet been demonstrated in the Strait of Georgia.

Crustaceans

Shrimps and prawns are bottom-dwelling animals as adults. The smaller shrimps prefer a sandy substrate, whereas the prawn, *Pandalus platyceros*, generally seeks a rocky bottom. Alteration of the bottom habitat by dumping various solid materials, such as mine tailings or dredge spoils, could affect populations of the various species of shrimp, especially *P. platyceros*.

Zoea (larval stage) of all shrimp and crab species have a pelagic phase. They could conceivably be affected by sea surface pollution, although this has not been recorded in the Strait of Georgia. The coonstripe shrimp, *Pandalus danae*, was once harvested in substantial amounts in Burrard Inlet. By about 1960, the species was no longer available there in commercial quantities (Butler 1980). The cause of the decline has not been explained, but the effects of waste disposal and heavy shipping in Vancouver Harbour could have contributed. The Dungeness crab (*C. magister*) continues to be present in Burrard Inlet, but its harvesting commercially has been banned because of pollution.

Discussion

The Strait of Georgia, as a whole, does not yet exhibit a degree of pollution that can be considered as alarming. This is related at least in part to the fact that it is favored with physical characteristics, such as relatively free connection with the open ocean, moderately big tidal range, and large freshwater runoff, which combine to replace the water from top to bottom at least once per year. Of course, like any other marine system, the Strait of Georgia has a finite capacity to assimilate or disperse the waste products and other materials introduced by humanity. So far, the assimilative capacity of the Strait has not been exceeded, except in local nearshore areas, to the point where other uses of the waters have been seriously jeopardized. This must be credited to the fact that the shoreline of the Strait of Georgia is not yet heavily populated or industrialized, at least in comparison with other coastal areas of the world, such as Europe and southeast Asia. Under the pressure of a larger population and heavier industrialization, the conditions might conceivably change rapidly.

The foregoing is the generalized picture of the state of pollution in the Strait of Georgia. As one examines the situation more closely, one can readily see some obvious exceptions. The most noteworthy of these is the effect that sewage has had on the harvesting of shellfish. Many of the shellfish areas in the Strait of Georgia are closed because of the high fecal coliform count in the waters. In virtually all cases, this can be attributed to anthropogenic sources, such as sewage disposal through outfalls, seepage from septic tanks, urban and agricultural runoff, recreational vessel discharges, and input by tributary rivers receiving the foregoing type of drainage. While corrective measures can usually eliminate or at least ameliorate point sources, such as outfalls discharging raw sewage, it is extremely difficult to eliminate such diffuse, non-point sources as agricultural runoff. As a result, even after sewage treatment plants and improved outfalls for better effluent dispersal are installed, there is often insufficient reduction in the coliform level of nearby waters to open shellfish areas to harvesting. One exception to this general rule in the Strait of Georgia is French Creek, near Parksville, where installation of secondary sewage treatment in 1978 was followed by restoration of water quality to meet shellfish standards. As a whole, however, fecal-coliform-contaminated runoff has contributed to closure of 12 836 ha of shellfish area along the shoreline of the Strait of Georgia, and 12 012 ha of this lie in Boundary Bay (B. Kay, Environmental Protection Service, West Vancouver, B.C., unpublished data).

The Fraser River is a major contributor of not only freshwater but also pollutants carried from urban municipalities and industries in the interior of British Columbia. The freshwater runoff overlies the seawater in a comparatively thin layer and mixes slowly with the seawater as it spreads over the Strait of Georgia and before it mixes into deeper water in the vertically mixed regions at the southern and northern approaches to the Strait. Pollutants concentrated in this water could have a serious impact on fish and other aquatic organisms in the Fraser River Estuary, as well as in the surface layer further offshore in the Strait. Moreover, any such pollutants can be carried into the bottom water by the vertical mixing process that takes place in the turbulent region of the southern entrance to the Strait. This applies also to such immiscible substances as oil that might be spilled on the surface from ships or shore installations.

While we are aware of the general state of pollution in the Strait of Georgia, we are not yet able to evaluate the "assimilative capacity" or to predict the short- or long-term impact of a major oil spill or the discharge of a large volume of toxic chemical. Virtually nothing is known about the sublethal effects of most chemicals and concerning the synergistic effects of a combination of chemicals and other substances reaching the sea. There is still a great deal that must be learned

about the physical behavior of the Strait of Georgia system before a suitable model with a predictive capability for such a purpose can be developed. Also, to develop a reliable mass balance for different pollutants, e.g. petroleum hydrocarbons, it is essential to have better data on inputs along the various pathways, i.e. ships, river runoff, shore installations, municipal sewers, urban runoff, and the atmosphere. We are still a long way off from achieving such a goal.

Conclusions

1) The Strait of Georgia as a whole is still relatively clean. There have been no major oil spills or other pollution incidents in the Strait or in its contiguous waters.
2) The Strait of Georgia is flushed comparatively frequently, with water in the upper layer, above the halocline, being replaced in a matter of months and deep water about annually. A crude estimation of the average residence time for freshwater in the upper layer is 9.6 mo, but this is probably longer than the actual residence time. About 90% of the water replacement in the Strait of Georgia takes place through the southern entrance where the channels are relatively deep. Because of regular flushing of the Strait of Georgia, pollutant levels or effects, e.g. oxygen deficiency, have not built up so far.
3) Pockets of pollution exist along the shoreline in urban and industrial areas as a result of input of sewage and such industrial wastes as pulpmill effluents.
4) A number of dumpsites in the Strait of Georgia receive dredge spoils regularly. The most heavily used ones are the Point Grey and Sand Heads dumpsites. No serious pollution problem has been identified with their use so far.
5) Sewage pollution has led to closure of numerous shellfish beds, because of excessive bacteriological contamination, around the perimeter of the Strait of Georgia. Oyster culture has been most seriously affected with about one-fifth of existing oyster leases closed. But the areas of potential oyster-growing grounds closed because of fecal pollution in the past is many times greater. Part of the closure is due to agricultural and urban runoff and, in some areas, to sewage discharges from recreational boating.
6) The Fraser River, as the river system with the largest drainage basin and greatest freshwater input, could be a major source of pollution if there were a high upstream input of contaminants by industries and urban communities. Because the river water flows over the surface of the Strait of Georgia without rapid mixing, a widespread impact from a toxic, riverborne pollutant on marine organisms could be expected in the upper layer of the Strait. At present, there is only a nominal degree of pollution in the river water from industrial wastes and domestic sewage introduced as far upstream as Prince George and in the lower Fraser River. The impact on living resources so far has been comparatively small, judging by available data.
7) Intensive vertical mixing by tidal turbulence at the southern entrance to the Strait of Georgia can introduce surface pollutants, including oil, into the deep water of the Strait.
8) There are no data from full-scale surveys of concentrations of the more persistent contaminants, such as petroleum hydrocarbons, organohalogens, and metals, to provide a baseline on water quality in the Strait of Georgia. Existing data on metals suffer from variable quality. Improving technology in sampling and analysis has led to lower contamination of samples and higher precision, resulting in more reliable data. A series of analyses over a period of years invariably shows a decline in measured concentrations of metals, but this is often due to improved techniques rather than to a decreasing trend in metal concentrations for a given area.
9) No detailed studies have been conducted on the sublethal effects on marine organisms of pollutants in some of the industrial areas such as Harmac and Powell River. The work conducted in industrial "hot spots" of Puget Sound (Malins et al. 1980) could be a useful model for such studies.
10) The wide range of pollutants into the Strait of Georgia may lead to synergistic effects on marine organisms from a combination of different pollutants, which could conceivably cause a greater ecological impact than predicted from results of standard bioassays on individual pollutants. Little is known about such synergism in the Strait of Georgia, if indeed it does occur there.
11) The greatest potential risk of pollution in the Strait of Georgia is posed by possible exploration for and exploitation of oil and gas in the geological strata known as the Nanaimo Basin underlying the Strait between the Gulf Islands in the south and Quadra Island in the north. Transportation of crude oil and products through this "inland passage" could likewise present a serious hazard. A major oil spill could have devastating effects in the surface waters and along the shoreline, at least in the short term, as well as possibly contaminating the deep water, with long-term effects, in the Strait of Georgia.

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Part 8 of this remarkable series is now available and the quality continues to remain as high as for Part 1 which appeared in 1948. In 1973, with the appearance of Part 6, the series departed from the phylogenetic order of presentation for it was decided to publish on an ordinal or family basis, as manuscripts became available. Part 8 follows this pattern and treats in depth the family Syngnathidae. The subfamilies Doryrhamphinae and Syngnathinae comprise 27 species of pipefishes and Hippocampinae the three species of seahorses that occur in the region. C. E. Dawson prepared excellent accounts for the pipefishes. These accounts are extensive (172 of the 198 pages) and beautifully illustrated with excellent drawings and photographs. R. P. Vari prepared the illustrated accounts of the three species of seahorses. The treatment of the seahorses is less extensive than that of the pipefishes, perhaps reflecting a more limited body of data for these fishes.

Canadians will find Part 8 of less interest than previous volumes of the series since only three species occur off Canadian shores — *Amphelikturus dendriticus* (Barbour), the seahorse pipefish, *Syngnathus fuscus* Storer, the northern pipefish and *Hippocampus erectus* Perry, the lined seahorse.

The *Fishes of the Western North Atlantic* volumes are invaluable contributions to ichthyology and the authors are to be congratulated on the quality of the presentations. Hopefully, the interval between the appearance of future volumes will be less than the 5 years which have elapsed since the publication of Part 7.

W. B. SCOTT

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Crabs and their Relatives of British Columbia. *Josephine F. L. Hart. B.C. Provincial Museum Handbook No. 40. 1982. 267 p., 102 fig. + 12 color plates. $5.00.*

Crabs are among the most abundant and obvious animals seen by people on the shore, by commercial fishermen, and by SCUBA divers. Dr Hart's timely handbook will be of use to people and to professional biologists attempting to identify crabs from surveys or sampling programs.

Probably the professional biologist will find the well-organized keys of most use, as the layman would find the anatomical terms required for identification heady. It might be difficult to "thumb through" the Handbook and identify a crab to species, but probably the correct genera might be located. The watercolor plates give the book an artistic feature not found in most of the other B.C. Provincial Museum handbooks. The prints are reminiscent of the beautiful handcrafted and colored drawings done by taxonomists of the last century. Unfortunately, many crabs are often adorned by algae, bryozoans, and other encrusting biota. The true colors of the exoskeleton are rarely obvious and possibly of limited value for identification purposes. The excellent line drawings, well-organized explanation of crab anatomy, and binomial keys are much more valuable. A systematist colleague was glad to see that groups are arranged phylogenetically.

Some features of the Handbook which could have used clarification for the benefit of the biologist are as follows. The synonyms given below the currently used name are not shown with their authors or dates of publication and so unfortunately further sleuthing would be needed to track down the taxonomic history of each species. The section on ecology and life history is adequate and peculiarities of crabs are suitably highlighted. However, more information or examples of life history could have been given using species common in B.C. rather than the Alaskan King crab.

Some minor points of dispute were observed but only three misprints. Omitting a description of the possible shells used by most of the hermit crabs was unfortunate. The presence of certain leeches on some crabs could have been noted, as sometimes they are quite obvious. Fisheries Officers would have been happier to see greater emphasis put on the size limits for Dungeness and rock crabs, as taking of small crabs is one of the most frequent offences they have to enforce, especially near cities. Finally, there was no mention of habitat loss which may be affecting crab populations in certain areas.

In summary this bargain-priced book is highly recommended for professional marine biologists and lay persons interested in crab identification. We are indebted to Dr Hart for bringing together her extensive knowledge of these animals, the study of which almost literally has been her life's work.

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V7V 1N6 (R473)

Books Received/Livres reçus

March–April/mars–avril 1983

Strait of Georgia Chinook and Coho Fishery. *A. W. Argue, R. Hilborn, R. M. Petermen, J. J. Staley, and C. J. Walters. Canadian Bulletin of Fisheries and Aquatic Sciences 121. Government of Canada, Fisheries and Oceans, Ottawa. 1983. 91 p. $8.95 (Canada); $10.75 (other countries).* In an effort to evaluate proposed regulations on sport and commercial fishermen, the authors developed a computer simulation model. They discuss the model with respect to an "enhancement" of chinook and coho in respect to regulations for these stocks. (R490)

Catalogue of the Living Bivalvia of the Eastern Pacific Ocean: Bering Strait to Cape Horn. *F. R. Bernard. Canadian Special Publication of Fisheries and Aquatic Sciences 61. Government of Canada, Fisheries and Oceans, Ottawa. 1983. 102 p. $8.00 (Canada); $9.60 (other countries).* This work consists of a systematic catalogue and primary bibliography. Included are synonymies for each species and updated distributions. Six replacement names and various changes of suprageneric categories are suggested. (R491)

Physiology and the Mariculture of some Northeastern Pacific Bivalve Molluscs. *F. R. Bernard. Canadian Special Publication of Fisheries and Aquatic Sciences 63. Government of Canada, Fisheries and Oceans, Ottawa. 1983. 24 p. $4.00 (Canada); $4.80 (other countries).* Equations describing the effects of water temperature, salinity, oxygen, and food availability on ventilation and oxygen consumption rates of nine species of bivalve molluscs are given. (R492)

Acid Rain. *Robert H. Boyle and R. Alexander Boyle. NLB (Nick Lyons Books), Schocken Books, New York. 1983. 146 p. $14.95 (U.S.) hardback, $8.95 (U.S.) paperback.* The material for this study was drawn from the authors' own reports, the scientific literature, and other published sources. It sets forth the scope of this environment problem and then outlines the delays and counter arguments encountered in trying to reach acceptable solutions. (R493)

Research on Fish and Wildlife Habitat. *Technical Editor William T. Mason, Consulting Editor Sam Iker. Office of Research and Development, U.S. Environmental Protection Agency, Washington, D.C. 1982. 248 p.* This monograph, produced cooperatively with the U.S. Fish and Wildlife Service, provides insights into research progress during the 1970s that has helped pave the way for a better environment for the 1980s. (R494)

Theory and Management of Tropical Fisheries. *Edited by D. Pauly and G. I. Murphy. International Center for Living Aquatic Resources Management (ICLARM) and Commonwealth Scientific and Industrial Research Organization (CSIRO). Printed in Manila, Philippines. 1982. 360 p. In U.S.A. $28.50 (paper), $32.50 (cloth) from ISBS, P.O. Box 1632, Beaverton, Oregon 97075; elsewhere $17.50 surface, $28.50 air (for paper) and $21.50 surface, $32.50 air (for cloth) from ICLARM.* Proceedings of the ICLARM/CSIRO Workshop on the Theory and Management of Tropical Multispecies Stocks, 12–21 January 1981, Cronulla, Australia. The book represents the current state-of-the-art. On a number of matters, the participants failed to reach a consensus. (R495)

Recherches sur la baie d'Hudson et la baie James/ Scientific Studies on Hudson and James Bays. *Naturaliste canadien 109 (3, 4), 1982. 725 p. (p. 301–1019). $28.* Sixty selected papers from a symposium held at the University of Guelph 28–30 April 1981 are published as two special issues of the journal Le Naturaliste Canadien (Revue d'écologie et de systèmatique). The ten sections covered are as follows: geology and geomorphology, climatology and permafrost, soils, vegetation, mapping and ecological land classification, physical oceanography, marine ecology, environmental impact of hydroelectric projects, wildlife biology, human ecology. (R496a, b)

Textbook of Fish Health. *Dr. George W. Post. TFH Publications, Inc., Neptune City, N.J. 1983. 256 p. $29.95 (U.S.).* An account of mechanisms and organisms that cause disease in fishes, with emphasis on the diseases of bacterial and viral origin. It covers history, signs, treatment, and distribution. In addition to 172 full color photos, there are 19 line drawings and bibliographies. (R497)

Handbook of Darters. *Dr. Lawrence M. Page. TFH Publications. Inc., Neptune City. N.J. 1983. 272 p. $29.95 (U.S.).* This book covers more than 100 species of darters found in streams of the eastern United States. Included are over 300 full color photographs and 89 distribution maps. It is primarily intended for students and ichthyologists. (R498)

Gazetteer of Undersea Feature Names 1983. *Advisory Committee on Undersea Feature Names, Canadian Permanent Committee on Geographical Names. Department of Fisheries and Oceans, Canadian Hydrographic Service, Ottawa, Ontario 1983. 191 p. $11.95 (Canada); $14.95 (other countries).*

This gazetteer covers water areas of interest to Canada. There is an alphabetical list of all approved names with designations identifying the nature of the feature to which each name applies. The reader is referred to the charts or maps on which each name might be found. (R499)

ANNOUNCEMENTS/AVIS

Conference on Copepoda

The Second International Conference on Copepoda will be held in Ottawa, Canada from August 13 to 17, 1984. There will be a panel discussion on Phylogeny of Copepoda and four symposia: Biogeography of Copepoda; Behavior Ecology; Growth, Life History and Culture; Morphology and Anatomy. In addition there will be five half-day sessions of contributed papers as well as a poster session.

The deadline for submission of abstracts is December 31, 1983; these will be printed before the Conference. All manuscripts will be published if submitted before the end of the Conference.

Persons interested in receiving future announcements and other information about the Conference are asked to write to: *Chang-tai Shih or Ian Sutherland, Invertebrate Zoology Division, National Museum of Natural Sciences, Ottawa, Ontario, Canada K1A 0M8.*

Freelance Scientific Editors

The Scientific Information and Publications Branch of the Department of Fisheries and Oceans seeks a contract scientific editor to work on Supplements to the *Canadian Journal of Fisheries and Aquatic Sciences*, Special Publications, and possibly some large Bulletins.

The editor will be responsible for assessing the scientific worth of manuscripts, guided by referees' advice, and for editing manuscripts to conform to the Branch's standards, especially ensuring that the presentation is succinct and comprehensible, and that publication deadlines are met.

We seek well qualified scientists with mature scientific judgment, clear insight into the research process, a strong sense of diplomacy, and ability to meet strict deadlines. People whose talents are restricted to polishing the writing would not meet our requirements. Candidates must be Canadian citizens or residents of Canada.

Interested candidates should send a copy of their résumé to *J. M. Reinhart, Scientific Information and Publications Branch, Department of Fisheries and Oceans, 240 Sparks St., Ottawa K1A 0E6.*

Conférence sur les copépodes

La Deuxième conférence internationale sur les copépods se tiendra à Ottawa du 13 au 17 août 1984. Une réunion-débat sur la phylogénie des copépodes auront lieu à cette occasion; aussi quatre colloques: biogéographie, éco-éthologie, développement, cycle biologique et culture, ainsi que morphologie et écologie. De plus, cinq séances d'une demi-journée seront consacrées aux communications scientifiques de même que la séance de démonstration.

Les résumés devront être envoyés au plus tard le 31 décembre 1983 et seront publiés avant la Conférence. Tous les manuscrits seront publiés s'ils sont remis avant la fin de la Conférence.

Pour recevoir les avis ultérieurs et de plus amples renseignements au sujet de la Conférence, on est prié d'écrire à: *Chang-tai Shih ou Ian Sutherland, Division de la zoologie des invertébrés, Musée national des sciences naturelles, Ottawa (Ontario) Canada K1A 0M8.*

Réviseurs scientifiques pigistes

La Direction de l'information et des publications scientifiques du ministère des Pêches et des Océans recherche un réviseur scientifique pigiste pour la révision des suppléments au *Journal canadien des sciences aquatiques et halieutiques*, des publications spéciales et parfois de certains bulletins volumineux.

Le réviseur devra prendre des décisions sur la valeur scientifique des manuscrits, en tenant compte des conseils des arbitres; il devra les réviser conformément aux normes de la Direction, en s'assurant tout particulièrement que la présentation est succinte et compréhensible et que les échéances de publication sont respectées.

Nous recherchons des scientifiques compétents qui ont un jugement scientifique éclairé, une bonne compréhension du processus de recherche, un sens aigu de la diplomatie et qui peuvent respecter des échéances rigides. Les personnes dont le talent se limite à polir le style ne répondraient pas à nos critères. Les candidats doivent être citoyens canadiens, ou résidents du Canada.

Les candidats intéressés sont priés de transmettre un exemplaire de leur *curriculum vitae* à *J. M. Reinhart, Direction de l'information et des publications scientifiques, Ministère des Pêches et des Océans, 240, rue Sparks, Ottawa K1A 0E6.*

COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

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Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States
C. P. Hawkins, M. L. Murphy, N. H. Anderson, and M. A. Wilzbach

An integrated study of the factors influencing the choice of the settling site of *Balanus crenatus* cyprid larvae **C. Hudon, E. Bourget, and P. Legendre**

Nutrient limitation in two arctic lakes, Alaska **G. A. McCoy**

Effects of low environmental pH on smolting of Atlantic salmon (*Salmo salar*)
R. L. Saunders, E. B. Henderson, P. R. Harmon, C. E. Johnston, and J. G. Eales

Experimental management of Oregon coho salmon (*Oncorhynchus kisutch*): designing for yield of information **R. M. Peterman and R. D. Routledge**

Towards a better definition of "metamorphosis" in *Coregonus* sp.: biochemical, histological, and physiological data **H. Forstner, S. Hinterleitner, K. Mähr, and W. Wieser**

An analysis of the Hecate Strait Pacific cod fishery using an age-structured model incorporating density-dependent effects **D. A. Fournier**

Deformation of the active space in the low Reynolds number feeding current of calanoid copepods **J. C. Andrews**

Origin, distribution, and postglacial dispersal of a swimbladder nematode, *Cystidicola stigmatura* **G. A. Black**

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Reproductive success of artificially hybridized golden trout (*Salmo aguabonita*) and rainbow trout (*Salmo gairdneri*) **R. Halliburton, R. E. Pipkin, and G. A. E. Gall**

Characterization of organic copper-complexing agents released by *Daphnia magna*
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Lipid quantification of freshwater invertebrates: method modification for microquantitation
S. E. Herbes and C. P. Allen

Movements of coho salmon (*Oncorhynchus kisutch*) fingerlings in a stream following marking with vital stain **J. H. Mundie and R. E. Traber**

Carrying capacity of an enhanced side-channel for rearing salmonids
J. H. Mundie and R. E. Traber

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Comment on use of allelic frequencies to describe population structure **C. Busack**

Reply **F. W. Allendorf and S. R. Phelps**

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The biology of lampreys. Volume 3 (M. W. Hardisty and I. C. Potter [ed.])
F. W. H. Beamish

Fisheries and Oceanography of the Strait of Georgia

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